THE LIFE HISTORIES AND REPRODUCTIVE STRATEGIES OF THREE SPECIES OF *RUMEX* L.

With 16 separate charts

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J. Dobinson

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ABSTRACT

The life history strategies, allocation of resources, mechanisms of reproduction and agricultural significance of *Rumex acetosella*, *R. crispus* and *R. obtusifolius* are considered.

Survivorship patterns for the three species are derived from a detailed study of approximately 900 individually marked plants over a period of almost three years. Concavo-convex survivorship curves were obtained, differing from the generally linear survivorship curves described to date for perennial species. The survivorship data imply that successive life stages differ in their survival rates. The differences in survival rate of life stages are related to the diverse types of life histories found amongst perennial plants.

The patterns of resource allocation in *R. crispus* and *R. obtusifolius* were derived from energy determinations of naturally growing plants at four plot sites. At higher plant densities, fewer plants flowered. The mean reproductive efforts of flowering plants for each species at each plot were similar over a wide range of plant densities. Within plots, smaller plants tended to have higher reproductive effort. The allocation of resources in *R. acetosella* was investigated experimentally. Energy determinations were used to assess the changing patterns of resource allocation under three stress regimes. Under higher stress levels, sexual reproductive effort increased in females but not in males whilst vegetative reproductive

effort remained constant. Radioactive tracer studies were used to estimate the cost of vegetative offspring to the parent plant.

The mechanisms of reproduction, particularly seed abscission and seed dormancy, were studied using a variety of techniques including scanning electron microscopy and wind tunnel tests.

The last section discusses the three species in an agricultural context. The severity of the "dock problem", existing control techniques and possible improvements to control techniques are considered. The potential for the biological control of the species is outlined.

CHAPTER I

GENERAL INTRODUCTION

I. INTRODUCTION

In advocating a Darwinian approach to plant ecology, Harper (1967) referred to two areas which had received little attention. These areas were the study of life history strategies and the allocation of limited resources to the processes of reproduction.

An understanding of life history strategies must be preceded by a knowledge of the mortality rates of different life stages. To date, there are few detailed studies of mortality patterns and life history strategies in plants (e.g. Sharitz and McCormick 1973; Sarukhán and Harper 1973; Sarukhán 1974). The paucity of such studies led Sarukhán and Harper (1973) to comment that the development of mathematical models to describe mortality in plant populations is secondary to discovery and analysis of the causes of mortality during different stages in the life of plants.

The description of mortality patterns in plants necessarily involves the detailed observation of marked individuals for extended periods. This has been carried out in the present study for approximately two and a half years on six natural populations of perennial plants. Over this

period the fates of nearly 900 individually labelled plants have been followed.

Harper (1967) stated that few attempts have been made to compare the ways in which different species of plant allocate their limited resources. Recently, however, there has been increasing interest in the concept of resource allocation, reproductive strategies and reproductive effort (Johnson and Cook 1968; Harper and Ogden 1970; Ogden 1974; Gaines *et al.* 1974; Raynal and Bazzaz 1975; Hickman 1975; Wilbur 1976). Williams (1975) and Harper (1967) have also drawn attention to the different roles of seed and vegetative reproduction in species which possess both. Various aspects of the costs, risks and benefits of these two modes of reproduction have been investigated by Smith (1972), Thomas and Dale (1975) and Abrahamson (1975). A preliminary investigation of the allocation of resources, and in particular reproductive effort, is presented below.

II. THE AIMS OF THE THESIS

The principal aim of the thesis is to investigate the life history strategies and allocation of resources in three closely related weed species in the genus *Rumex: R. acetosella, R. crispus* and *R. obtusifolius*. A secondary aim is to discuss the status of these three plants as weeds, and to review and suggest improvements to the techniques developed to control them.

The thesis is divided into four main areas: an introduction to the species being studied and the study area

and methods; a discusson of survival rates and their relationship to life histories; a discussion of reproductive effort and the mechanisms of reproduction; and finally a section dealing with *R. acetosella*, *R. crispus* and *R. obtusifolius* in an agricultural context.

The discussion of survival rates argues that contrary to the suggestion by Sarukhán and Harper (1973) that plant populations generally present linear survivorship curves, survivorship curves are generally composite. Survivorship curves which are not linear imply that mortality rates differ between life stages. As life histories evolve in response to the relative mortality of each life stage (Stearns 1976), a knowledge of the mortality rate of each life stage is essential to an understanding of life history evolution. The survival rate curves associated with various survivorship patterns are described for a range of species (including the three *Rumex* species studied here), and related to diverse types of perennial life histories.

The section dealing with reproductive effort describes the allocation of resources to reproduction under a variety of conditions for each species. For *R. acetosella*, the relative costs, risks and ecological and genetical benefits of vegetative and sexual reproduction are discussed. These are related to the changing pattern of resource allocation under various levels of environmental stress. The section is concluded with a description of the reproductive mechanisms of each species.

The final section attempts to assess in an agricultural context the extent and severity of the damage

done by these three *Rumex* species. The advantages and disadvantages of a variety of cultivation techniques and herbicides (in particular Asulam) are discussed. Finally the potential for biological control of these three species is considered.

CHAPTER II

THE PLANTS BEING STUDIED

I. INTRODUCTION

A comparative approach to the study of population dynamics and the strategies and tactics of the reproductive process should be made on a group of common, closely related species which are basically similar but display contrasting life-cycle strategies. For practical reasons, the species should produce discrete vegetative propagules connected to the parent by above ground structures and become quickly independent of the parent, seeds which are not subject to extensive migration and present no serious dormancy problems, and some morphological character that permits the age of the plant to be measured (Sarukhan and Harper 1973).

These requirements and others which facilitate the practical aspects of a study such as this are not all possessed by the three species being studied. However, the three species have enough of the requirements to enable interesting comparisons to be made between them. Their generally similar gross morphology facilitates comparative measurement and all three species grow at sufficiently high densities to make the study of individual plants practicable. Furthermore, all three species are of economic interest because of their weedy nature.

Plate 1. *R. acetosella* plant. A vegetative offspring is shown arising from an adventitious root bud on the left. Bar = 10 cm.

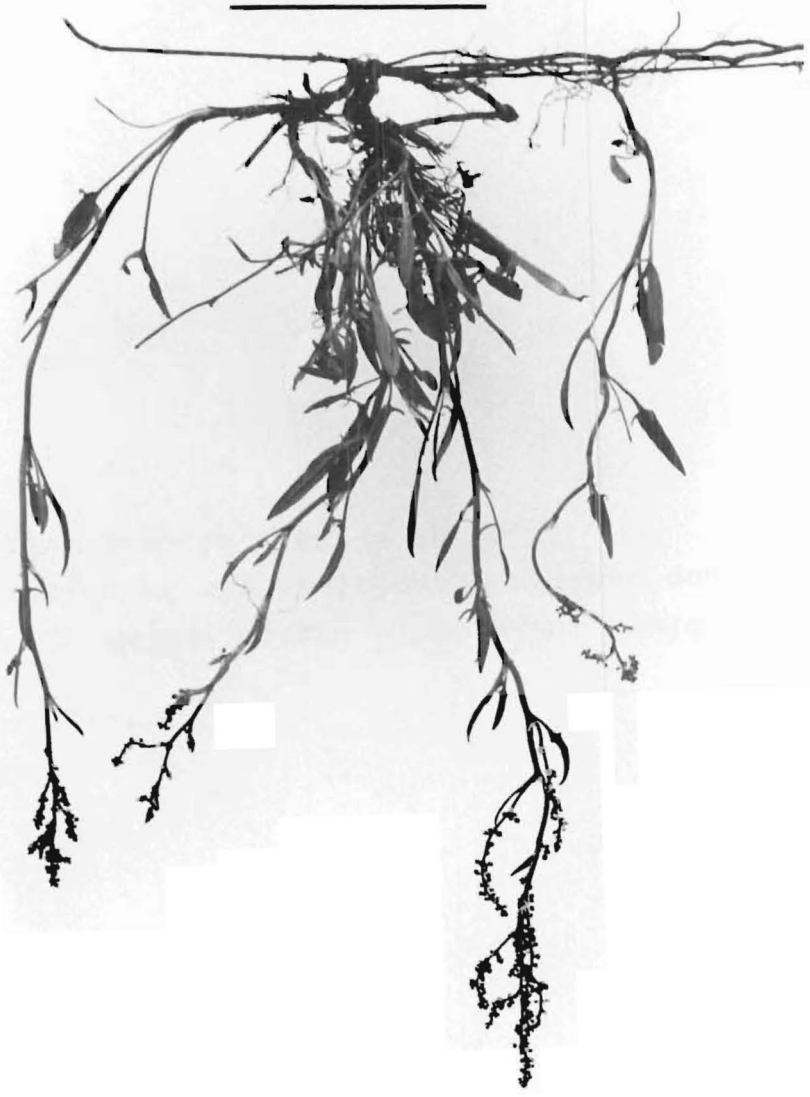


Plate 2. *H. erlospus* plant. This plant would be given a classification of six as it has more than one shoot and reproductive panicle. Bar = 10 cm.

Fig. 3. *R. obtusifolius* plant. Bar = 10 cm.

The three *Rumex* species are closely related, although *R. acetosella* is in the subgenus *Acetosella* whilst the other two species are in the subgenus *Acetosa*.

R. acetosella is a dioecious perennial herb which reproduces vegetatively by adventitious root buds (Plate 1). *R. crispus* and *R. obtusifolius* are also perennial herbs, with erect flowering stems. The leaves form a basal rosette (Plates 2 and 3). The tap root of *R. crispus* is smaller and less branched than that of *R. obtusifolius*.

II. THE ORIGIN AND DISTRIBUTION OF THE THREE SPECIES

In New Zealand all populations of *R. acetosella* are angiocarpic and hexaploid. Harris (1969) concluded that naturalized populations of *R. acetosella* originated in South and South-East Europe where the species are predominantly angiocarpic and hexaploid, and came here via North America and areas of the Southern Hemisphere where the species are also predominantly angiocarpic and hexaploid.

R. obtusifolius is indigenous throughout Europe except the Mediterranean region (Cavers and Harper 1964) and has been introduced to many other parts of the world including New Zealand. Cavers and Harper (1964) stated that the origin of *R. crispus*, one of the five most widely distributed plants in the world, can no longer be recognised. Healy (1969) suggested that these three species were originally brought to New Zealand as contaminants in seed. Thomson (1922) states that the "obnoxious weed" *(R. obtusifolius)* was introduced into the country at an early period of settlement, as few samples of grass or other agricultural seed brought

from Britain were free from it. An interesting anecdote of Darwin's, recounted by Thomson, may account for the introduction of *R. obtusifolius* into at least one part of this country. Darwin, who visited the Bay of Islands in 1835, said: "The common dock is also widely disseminated and will, I fear, forever remain a proof of the rascality of an Englishman, who sold the seeds for those of the tobacco plant". Colenso refers to a similar incident in 1845 and describes a "horrid" dock, so thick he could scarcely make his way through, which "seeding largely was carried down the rivers and filled the country". Thomson, referring to *R. crispus*, stated that it was generally distributed in the north in 1880. Cheeseman (1906) reported that this species was abundant in fields and waste places in all parts of New Zealand. Thomson also reported that *R. acetosella* was one of the most abundant weeds in the country.

At present, all three species are widely distributed and common in New Zealand. *R. acetosella* is found over a wider range of habitats than the other two species, which tend to follow man. Harris (1969) stated that *R. acetosella* occurs from sea level to the limits of the snow-tussock grasslands. However, Healy (1969) stated that above about 800 m there is a marked decrease in the frequency of the species with increasing altitude. Above about 1700 m *R. acetosella* is infrequent, only being found near huts and tracks where it has been carried by trampers and animals.

It is probable that neither winter cold nor altitude impose limitations on the distribution of *R. crispus* or *R. obtusifolius* in New Zealand as both species have been found

at high altitudes and at up to 60° of latitude in the Northern Hemisphere. The distribution of these two species in New Zealand may be associated with the presence of disturbed habitats, usually in conjunction with agriculture. According to Healy (1969) the distribution and abundance of the three species in Canterbury is as follows: *R. acetosella* is frequent and widespread on coastal sands and gravels, and abundant and widespread in artificial and tussock grasslands, cultivated and waste land. The other two species are widespread in a variety of habitats. They are abundant in waste places and untended land, frequent in cultivated land, occasional in artificial grassland, riverbeds and gardens. Both species are also common in pastoral habitats and rare in coastal sands and gravels.

R. acetosella is most common in soils of an acid type (King 1966), most plants being found in soils with a pH between 5.0 and 6.0. It grows preferentially on well drained, lighter sandy soils. In New Zealand it is frequently found in disturbed habitats or areas of low fertility (where it replaces high fertility species), on lighter shingly soils of coastal and inland plains and the sunny aspect of ploughable hill country (Healy 1969).

Cavers and Harper (1964) found that *R. crispus* and *R. obtusifolius* grew on all soil types except peat. On acid mineral soils, both were slow growing, *R. obtusifolius* growing better than *R. crispus*. They also found both species growing in widely different plant communities in Britain. In New Zealand, both species are found amongst garden plants, arable fields, grassland and waste places. *R. acetosella* is

principally found on grasslands, waste land and sand dunes.

III. THE LIFE HISTORY OF EACH SPECIES

R. acetosella is a perennial which produces seeds and vegetative propagules in the form of adventitious root buds (Raju Coupland and Steeves 1966). The seeds are able to germinate throughout the year. It is probable that there is a small flush of seedlings in the spring. After a seedling has become established, shoot number is rapidly increased under favourable conditions. Where poorer conditions prevail the number of shoots remains low. By summer, when flowering takes place, the plants have usually produced horizontal roots from which adventitious root buds arise. These develop into plants which soon become independent of the parent and may be capable of sexual reproduction in the same season.

The life histories of *R. crispus* and *R. obtusifolius* are similar to each other. Seeds may germinate at any time of the year, although there is often a flush of seedlings in the spring and in the middle of autumn. After establishment, a rosette of leaves is formed. This is followed by a period during which floral induction and initiation takes place. A period of growth, panicle emergence, anthesis, fertilization and seed maturation completes the cycle. If conditions are favourable the plant enters a rosette stage and overwinters until the middle of the following spring when regrowth starts again. Listowski and Jackowska (1964) conducted experiments which showed that *R. obtusifolius* behaves as a long day plant after vernalization, short days

having an inhibitory effect. This cycle may be repeated for a number of years. Cavers and Harper (1964) reported that *R. crispus* plants have a tendency to die after reproducing seed whilst Chancellor (1970) stated that plants frequently die after flowering. In *R. obtusifolius* the tendency is not as marked. *R. crispus* is also described as behaving as an annual in arable land. I did not observe mortality after one year or flowering.

Under certain conditions panicles may be initiated twice in one season, although this was not often observed in *R. crispus* plants unless they had been damaged.

In *R. crispus* and *R. obtusifolius*, seeds fall from the panicle from the time they first mature until the end of winter, by which time the panicle has usually become so weakened that it collapses. The rate of seed fall is not constant. For both *R. crispus* and *R. obtusifolius* most seeds fall after some months on the panicle, although some seeds fall throughout the year. Plants are frequently able to set seed in the season in which they germinate, but may not flower for the first few seasons under less favourable conditions.

Root growth is greatest in the spring (Cavers and Harper 1964). After the first season, the roots commonly initiate adventitious shoots which may thicken. In damaged or older plants which have a number of shoots the primary root may become fragmented, the portions being essentially independent in function.

Table 1. THE PRINCIPAL DIFFERENCES IN THE LIFE HISTORY AND REPRODUCTIVE BIOLOGY OF THE THREE SPECIES

SPECIES	LONGEVITY	SEXES	REPRODUCTION	SEEDS
R. acetosella	Shoots tend to be annual, although the genotype is long lasting.	Essentially dioecious.	Principally by vegetative root buds, although large numbers of seeds are produced.	No abscission mechanism or special organs for dispersal. Seeds are small 1.3 - 1.5 mm long.
R. crispus	Perennials, but behave as annuals under adverse conditions.	Predominantly hermaphrodite flowers.	Exclusively by seed under natural conditions. May be propagated from root cuttings in cultivated situations.	Abscission zone present. Large valves and tubercles to increase dispersal by wind and water. Large seed up to 2.5 mm long.
R. obtusifolius	Perennials, very long lasting.	Predominantly hermaphrodite flowers.	As for *R. crispus*.	Abscission zone present. Large toothed valves bearing tubercles. Teeth may increase the probability of animal dispersal. Large seed up to 2.5 mm long.

IV. VEGETATIVE REPRODUCTION IN THE THREE SPECIES

R. acetosella reproduces principally by the production of vegetative offspring from adventitious root buds (Table 1). The number of plants may also increase when branches developed on older shoots near the surface take root at the nodes (Kiltz 1930). Although it did not occur on any of the plants being studied in the field, it did occur on the plants grown in pots for the radioactive carbon study. Under harsher conditions the above ground parts wither in the late summer, leaving the root system to produce new shoots the following season by the production of adventitious root buds. The length of time over which the colony is able to persist is not known, but it is at least some years.

The contribution that sexual reproduction makes to the maintenance of the population is small compared with the contribution from vegetative reproduction (Putwain 1970). The vegetative mode of reproduction not only increases the population under natural conditions but allows the re-establishment of plants from root fragments after cultivation. However, *R. acetosella* is unable to survive continued cultivation as its regenerative powers are limited.

Under natural conditions *R. crispus* and *R. obtusifolius* reproduce only by seed.

V. REPRODUCTIVE BIOLOGY OF THE THREE SPECIES

R. acetosella is essentially dioecious although hermaphrodite and monoecious intersex plants do occur (Putwain and Harper 1972). The males and females are

readily distinguishable at flowering. *R. crispus* and *R. obtusifolius* have predominantly hermaphrodite flowers. *R. obtusifolius* is highly self fertile whilst *R. crispus* shows variable self fertility (Cavers and Harper 1964). Outcrossing has been shown to be necessary in at least one case for *R. crispus* (Mulligan and Findlay 1970). Reproduction in both species is amphimictic. Hybridization between the two species is reported to be common (Lousley 1939), although not hybrids were common in the one site of this study where both species grew together. All three species are predominantly anemophilous. Insects, usually bees, occasionally visit the flowers for pollen. There is no nectar (Cavers and Harper 1964).

VI. SEED PRODUCTION AND MORPHOLOGY

The "dispersal unit" of *R. acetosella* is an achene with three closely adherent inner perianth segments. The inner perianth segments but not usually the pedicel remain attached to the seed. The dispersal units of *R. crispus* *R. obtusifolius* consist of an achene enclosed in the three inner perianth segments or tepals. These perianth segments are referred to as valves. The abaxial perianth segment bears a tubercle on its midrib. The tubercles on the other two perianth segments remain rudimentary. The outer perianth segments fail to develop and remain as tiny projections at the base of the inner perianth segments. Part of the pedicel remains attached to the perianth segments. The achenes of *R. crispus* and *R. obtusifolius* are between 3.0 and 3.5 mm long.

The species vary in their seed production. Large *R. acetosella* plants may ripen up to 6,000 seeds in a year whilst *R. crispus* plants may produce as many as 40,000 seeds. *R. obtusifolius* may produce up to 60,000 seeds per plant each year.

CHAPTER III

STUDY AREA AND METHODS

I. FIELD PLOTS

(1) Introduction

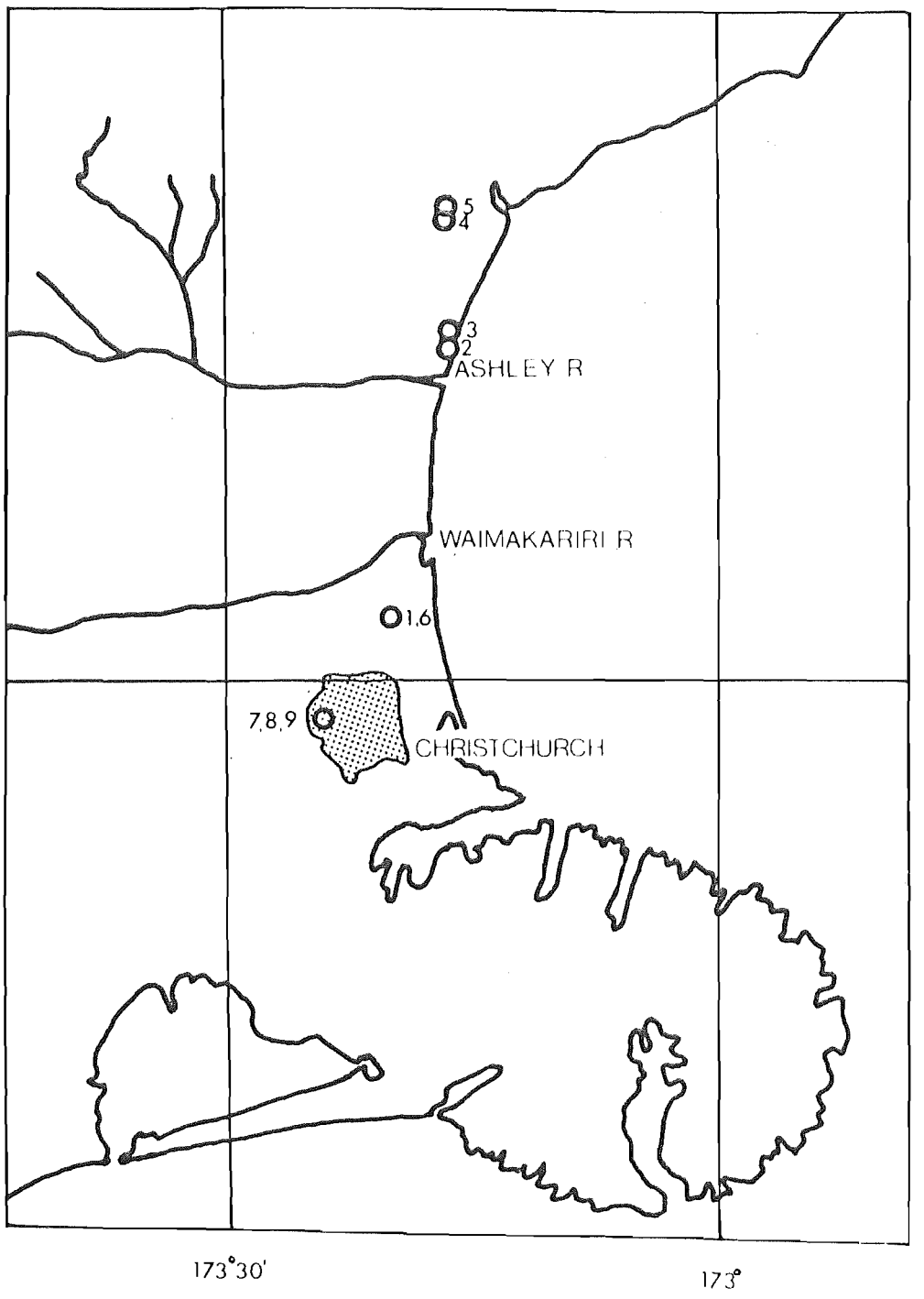
Two natural and one experimental population of each of the three species were studied. The natural populations were chosen to reflect the widest range of plant performance and population density possible among available sites.

The comparison among each of the three species at three sites would have resulted in nine different sites. This number was reduced by selecting one area where *R. crispus* and *R. obtusifolius* grew together, and by planting all three species at the nursery site. *R. acetosella* was studied in two field plots and at the nursery site.

Thus the study was made on nine plots at six sites (Map 1).

(2) Location of Plot Areas

Plot	Species	Property Owner and Location	Latitude and Longitude
1	C	Mt Stuart, Spencerville	43°28'S 172°E
2	C	Mr Ashworth, North of Saltwater Creek	43°15'S 172°43'E
3	A	As above (second site)	
4	A	Mr Alloway, North of the Kowai R.	43°11'S 172°44'E



Map 1. Locations of the six study sites.

Plot	Species	Property Owner and Location	Latitude and Longitude	
5	O	Mr Alloway, North of the Kowai R. (second site)	43°11'S	172°44'E
6	O	Mr Stuart, Spencerville	43°28'S	172°E
7	A	Nursery grounds, University of Canterbury	43°31'S	172°35'E
8	O	As above		
9	O	As above		

(3) The Establishment of Field Plots

Once the general area in which each plot was to be located had been chosen, an estimate of the density of the plants being studied was made to determine the ideal plot size. The plots had the following overall areas:

Plots 1 and 6	225	square metres
Plot 2	100	square metres
Plot 3	100	square metres
Plot 4	70	square metres
Plot 5	150	square metres

Around the operational area of each plot a one metre wide strip was left to reduce any unwanted effects from the enclosing fence and to provide a walkway. Immediately outside this strip a fence was erected.

Depending on the results of the first estimate of plant density, a grid with lines 1 metre, 50 centimetres or 10 centimetres apart was set up on each plot so that about ten plants were contained within any one square on the grid. Thus ten grid squares or quadrats contained about 100 plants. Randomly chosen quadrats were located and marked with a metal peg. Where the total number of plants

in the ten quadrats was less than 100, further quadrats were added until 100 plants had been located.

In plots 3 and 4, the location of every *R. acetosella* plant was marked on a 1:1 scale map for every 10 centimeter square quadrat being used, and every plant was labelled with a jeweller's label which had been numbered and then plasticized to prevent it from rotting.

The positions of plants of the other two species in the remaining plots with larger quadrats were recorded in centimetres East and centimetres South of the quadrat marker. Plants were also marked with large metal labels pushed into the ground near the plants. A photographic record was kept of each quadrat. **See Appendix 1 for plot details.**

(4) Description of Plot Areas

Plots 1 and 6 were located in the centre of a dairy pasture a small distance from a slight depression running diagonally across the field. As this area was below the top level of a large drain running nearby, the lower half of the field was frequently flooded, sometimes for several winter months. During the two years previous to the observations, the plot site had been used for non-intensive grazing. *R. crispus* and *R. obtusifolius* were the most common weeds amongst the perennial grasses of this field.

Plot 2 was in a depression between two rows of sand dunes. The depression and the sandy loam to clay loam soils of this site resulted in poor drainage of the area, the ground being waterlogged throughout the wetter months. The level of weed infestation prior to and during the study was very high, so the area was only marginally suitable for sheep

grazing. In an attempt to reduce the level of weed infestation, the owner cultivated or disced the whole area frequently and resowed it with grasses or rape. This had not been successful in reducing the numbers of *R. crispus* or *Plantago major* and *P. minor* plants, the two other common weeds.

Plot 3 was located within half a kilometre of plot 2 but was completely different in terms of soil type, drainage, cultivation and grazing regime. This plot was on top of one of the lines of consolidated sand dunes bordering the depression in which plot 2 was situated. Because of its elevated position and the sandy soil, the site was very well drained. The soil layer was very thin and had low nutritional levels. After discing two years before the study was undertaken, the field was resown in perennial grasses. *R. acetosella* was the principal weed species, *Plantago major* being the only other significant weed.

The other *R. acetosella* plot, plot 4, was located on the slope of an old river terrace about 200 m from the Kowai Stream. *R. acetosella* was the most abundant plant along the site of the river terrace, the areas above and below the step being sown in perennial grasses. For some years before the study was undertaken, this area had been grazed by cattle and left uncultivated.

Plot 5 was located in an uncultivated field used for grazing cattle. Because of the thistle problem in this field, it was mown once a year before the thistle seed matured. The field was in poor condition and infested with large numbers of *R. crispus*, *R. obtusifolius* and *Cirsium arvense* plants. Only *R. obtusifolius* was observed at this site because the mowing resulted in a severe setback for *R. crispus* plants.

The *R. obtusifolius* plants returned to their normal condition within a few weeks of being mown.

The experimental plots 7, 8 and 9 were situated on flat, well cultivated land within the grounds of the University of Canterbury. The area had lain waste for some years prior to the study although it was occasionally used for grazing horses.

(5) Physical Characteristics of the Soil at Each Plot

At each site, five randomly chosen samples of approximately 600 cubic centimetres were taken with a soil core sampler from the top 10 cm of the soil. After the removal of stones and macro-organic matter, each sample was dried in a forced air drying oven, mixed and passed through a 2 mm sieve and divided into four subsamples.

To measure water holding capacity, three subsamples were used. Distilled water was gradually mixed into each of these until the soil just glistened and would no longer adhere to a spatula held vertically. Hydrogen ion concentration was measured with a pH meter for each of the subsamples. One of the three subsamples was diluted 1:5 with distilled water from its original water holding capacity. The sample was filtered using a millipore filter, and the conductivity of the filtrate measured. The weight of a fourth subsample was measured from each of the original prepared samples. Each subsample was placed in a pre-weighed crucible and heated in a muffle furnace for 20 hours at a temperature of 380°C, cooled and reweighed. The percentage weight loss was calculated and substituted for x in the following equation (Ball 1964):

Per cent organic carbon = 0.458X - 0.4

The water table level was measured by digging a hole at every plot site. After 4 to 6 hours, the level of water in the holes was measured at all plots on the same day.

T-tests were carried out on the water-holding capacity, conductivity and organic content. A principal components analysis was also carried out on the results using the D.S.I.R. PCOMP file.

II. LIFE HISTORY AND SURVIVORSHIP DATA

(1) Population and Individual Plant Surveys

All labelled plants in each plot were surveyed and plants appearing since the last survey were labelled and surveyed.

The information recorded about each plant was divided into three sections: general plant data and location, and vegetative and reproductive shoot details. General plant data included the number of shoots, the number of reproductive panicles in each shoot and an arbitrary classification of the developmental level in functional terms. Class 1 consisted of plants with up to two leaves. Seedlings were not included in this class as they were too numerous to be surveyed by the techniques used to record data about individual plants. Seedling turnover was recorded using the techniques outlined below. Larger plants with one vegetative shoot (a rosette of leaves originating from one meristem) were placed in class 2, plants with more than one vegetative shoot into class 3. Class 4 was made up of damaged or otherwise abnormal plants. Class 5 consisted

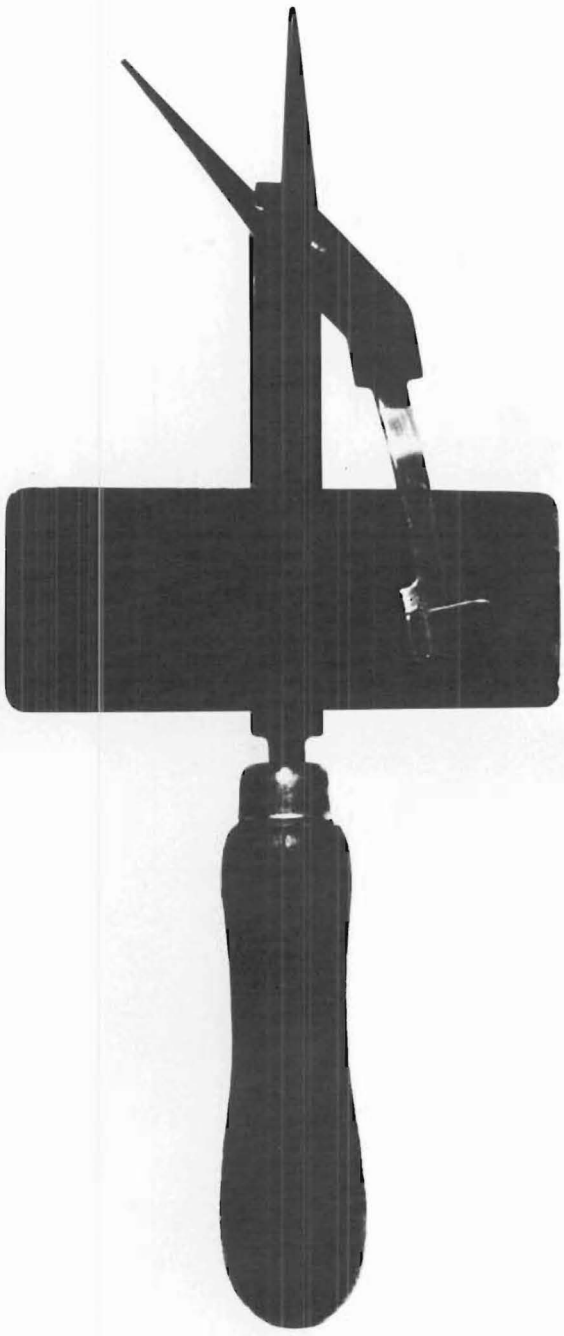
of plants without vegetative shoots and only one reproductive panicle. Class 6 contained plants with more than one reproductive panicle and without vegetative shoots. Class 7 consisted of plants with more than one vegetative and one reproductive shoot. It was subsequently verified that this arbitrary classification effectively divided plants into developmental stages except for classes 6 and 7. The presence or absence of vegetative shoots in plants with reproductive shoots indicated seasonal advancement rather than developmental status.

The details of each vegetative shoot were recorded separately. Attempts to follow the fate of particular shoots from survey to survey were abandoned as unreliable because of the large number of shoots in some plants, the apparent movement of growing shoots and a rapid growth rate which made the use of shoot markers impractical. For *R. crispus* and *R. obtusifolius*, the leaf blade length and width and petiole length were measured to the nearest half centimetre. In *R. acetosella*, only the leaf blade length was measured as this is directly related to leaf area. Petiole length was not recorded in *R. acetosella* because it was difficult to measure in many plants.

Leaf measurements were made to the nearest millimetre using the calipers illustrated in Plate 4. The calipers measured twice the length of the measured leaf and punched this length on to a card mounted on the platform.

The same reproductive shoot details were recorded for all three species. The overall height of the panicle and

Plate 4. The calipers used to measure *R. acetosella* leaves in the field. (× 1).



the lengths of the secondary and tertiary branches were measured. The number of whorls of seed and the number of seeds in three randomly chosen whorls were counted. It was possible to count the number of seeds which had dropped as the proximal portion of the pedicel remained attached to the panicle. The sex of *R. acetosella* plants producing flowers was noted.

(2) Span of Study and Survey Times

A number of surveys were carried out on each plot between 1974 and 1976. Winter flooding at the site of plots 1 and 6 delayed the initial survey, and farm requirements terminated the study at an earlier date than anticipated. See Appendix 2 for survey dates.

The extended time taken to complete a single survey (up to seven weeks) precluded surveys of all plots being carried out almost simultaneously. When flooding or bad weather prevented complete surveys from being taken abbreviated surveys were conducted; the presence of plants, their arbitrary classification and the presence of new plants were recorded.

(3) Seedling Dynamics

The behaviour of seedling populations in each plot was observed over one season. Seedling sample areas were located within the operational area of each plot, excluding quadrats containing labelled plants. Five randomly located soil core samples were taken at each plot every month for three months during one growing season. Cores were taken with a 10 cm × 10 cm core sampler sunk to a depth of 5 cm. Seedlings were removed from the sample and counted.

(4) Estimating Leaf Turnover Rates

In order to measure the maximum rate at which leaves were produced and lost during the height of the growing season, individual leaves were marked and observed at intervals. The experiment was carried out at the planted *R. acetosella* plot and at *R. crispus* and *R. obtusifolius* field plots.

Leaf turnover rate was measured by marking the youngest leaf in each shoot with a coloured ring (or in *R. acetosella* by punching a small semicircle out of the leaf). After 50 days, the number of new leaves per plant was counted.

III. THE ALLOCATION OF RESOURCES WITHIN THE PLANT

(1) The Allocation of Resources in Field Populations

Ten whole plants were collected per harvest from each plot at intervals over the reproductive part of the life cycle of each species. The ten plants were chosen by randomly selecting quadrats in the plot area, excluding those used in the population dynamics survey, until ten plants had been harvested. See page 84 for dates

The plants were washed free of soil, classified according to the outline in the population dynamics surveys and divided into the following parts: roots and stems, rosette leaves, panicle leaves, panicles and seeds (including flowers). The roots and stems were impossible to separate in plants which have more than one shoot. The roots and stems, and panicles were chopped up and all parts of each plant were separately dried to constant weight in a forced air drying oven at 70°C.

In some cases the bulk of the plant was too large to manage conveniently. In such cases the total wet weight of each part was determined, and a subsample of convenient size taken.

After drying, all parts of the plant were weighed and subsampled. The subsamples were ground to a coarse powder in a Watson Victor grinder and burnt in a Gallenkamp ballistic bomb calorimeter. Usually it was only practical to measure the energy content of each plant once or twice. To maintain accuracy, the calibration on the bomb calorimeter was checked at intervals by burning known weights of benzoic acid, and by making a number of energy determinations on single homogeneous samples.

(2) The Allocation of Resources to Sexual and Asexual Reproduction in *R. acetosella*

Two experiments were carried out which measured the proportion of energy allocated to seeds and/or vegetative offspring in *R. acetosella*. The first of these measured the energy content of the parent plant, its seeds and reproductive organs and vegetative offspring under various conditions. The second was designed to differentiate between the total energy present in the vegetative offspring of a particular parent plant and the energy it had received from the parent plant.

(a) The total energy present in parents, seeds and vegetative offspring of *R. acetosella* plants under three stress regimes: Ninety *R. acetosella* plants were grown from seed in growth rooms at 20°C with a 16 hour day length. The ninety plants were divided into three equal groups and a

different stress treatment imposed on each group by varying the pot size. The smallest pots imposing the greatest stress had a volume of 50 mℓ, the medium pots a volume of 400 mℓ, and the largest pots contained 900 mℓ. The ratio of the pot volumes was therefore 1:8:18.

Eight harvests of three plants were made from each stress treatment approximately every 16 days during the flowering season or whilst adventitious root buds were being produced. Three plants from each stress treatment were chosen randomly at each harvest. After each harvest the position of the pots in the trays was rotated.

Immediately after harvesting, each plant was removed from its pot and carefully washed free of sand and peat. The sex of all post-flowering plants was determined. The length of each leaf was measured to enable the total leaf area of the plant to be calculated. The parent plant and any vegetative offspring were separated into leaves, reproductive panicles, fruit, and root plus stem. Because it is impossible to assign connecting roots to a particular plant, these were included with the roots of the parent plant. Each part was dried in a forced air drying oven at 70°C to constant weight, weighed and ground to a fine powder in a pestle and mortar or a Watson Victor grinder, and the calorific value determined with a Gallenkamp ballistic bomb calorimeter. Replicate determinations were made on each sample where there was sufficient material. Heat liberated by the formation of nitric and sulphuric acid during combustion was not corrected for as Harper and Ogden (1970) had conducted similar tests and found that this never accounted for more than 0.25% of the total heat released.

(b) The movement of metabolites between the parent and vegetative offspring using radio active carbon as a tracer: ^{14}C was used to detect the movement of metabolized carbohydrates within and between the parent plants and their vegetative buds. Two experiments were conducted.

The first experiment determined the optimum time to count ^{14}C activity. The second experiment used this time to measure translocation between the parent and the offspring at different stages of vegetative bud development.

To determine the optimum time for the absorption of radioactive CO_2 by the parent and its translocation to the offspring, whole parent plants were sealed in plastic bags. Half a millilitre of radioactive CO_2 with an activity of one microcurie per millilitre was injected into each bag after most of the air had been removed from the bag. The bags were removed after one hour. After 0, 2, 4, 6, 8 and 10 days, the parent plants and their offspring were harvested separately. These were dried separately to constant weight, weighed and automatically oxidized and prepared for the scintillation counter. After counting, the percentage efficiency of recovery was calculated using a second degree polynomial. This was used to calculate the radioactive disintegrations per minute.

After establishing that the optimal sampling time was five days, the major part of the experiment was carried out.

All plants that had flowered were sexed, and in each pot a vegetative offspring that was isolated and could be bagged easily was marked.

For male and female plants and plants of unknown sex the marked offspring were ranked by size. The plants of

unknown sex were grouped into pairs with offspring of approximately the same size. The parent in one pot of the pair was injected with radioactive carbon-dioxide whilst the offspring in the other pot was injected. For plants of known sex, two male and two female plants, all with offspring of a similar size, were grouped together. Both the parents and offspring of all plants were harvested and their radioactivity measured. This allowed comparisons of the movement of resources between parents and offspring for both sexes and different offspring sizes to be made.

A total of 26 plants were tested, of which 5 could not be sexed.

IV. SEED GERMINATION

(1) Methods Used to Test Seed Germination

Three seed germination experiments were conducted. Variations from the basic techniques outlined below are described separately.

To prevent fungal contamination and damage to germinating seed (encountered in extended germination tests by Cavers and Harper 1966), sterile conditions were employed. In cases where it was necessary to remove the perianth, the seeds and perianths were rubbed on a no. 10 wire mesh and separated manually.

Seeds with or without perianths were washed in a dilute solution of sodium hyperchlorate ("Janola" diluted 1:6 with distilled water) for five minutes. They were then rinsed for five minutes in sterilised water. Fifty seeds were sown on to autoclaved filter papers dampened with

sterile water.

In their review, Cavers and Harper (1966) concluded that the following factors increase the percentage of germination: low temperature pretreatment, mechanical or chemical scarification (for example, brief exposure to sulphuric acid), exposure to light, and alternating temperatures, particularly with exposure to light. Steinbauer and Grigsby (1960) found that storage for one year did not decrease germination percentages. These results were used as a guide towards achieving maximum germination. Variations in light and temperature were employed to maximize germination percentages. Preliminary trials had determined that for seeds with the perianth segments removed, germination percentages reached 100% within 12 days. Up to 82% of seeds with the perianth segments germinated after 16 days. In both cases, there was no cold pretreatment or mechanical or chemical scarification.

Because the experiments on seed germination were mostly comparing germination rates or percentages within rather than between experiments, the exact duplication of conditions between experiments was not essential. Gill's (1938) expedient of using a windowsill for germination tests provided the required conditions conveniently. Where it was necessary to compare results between experiments, growth room facilities were used.

The period for which seeds were stored prior to germination varied with each experiment and is stated in each case.

(2) Establishing Maximum Germination Percentages for *R. crispus* and *R. obtusifolius* Seed

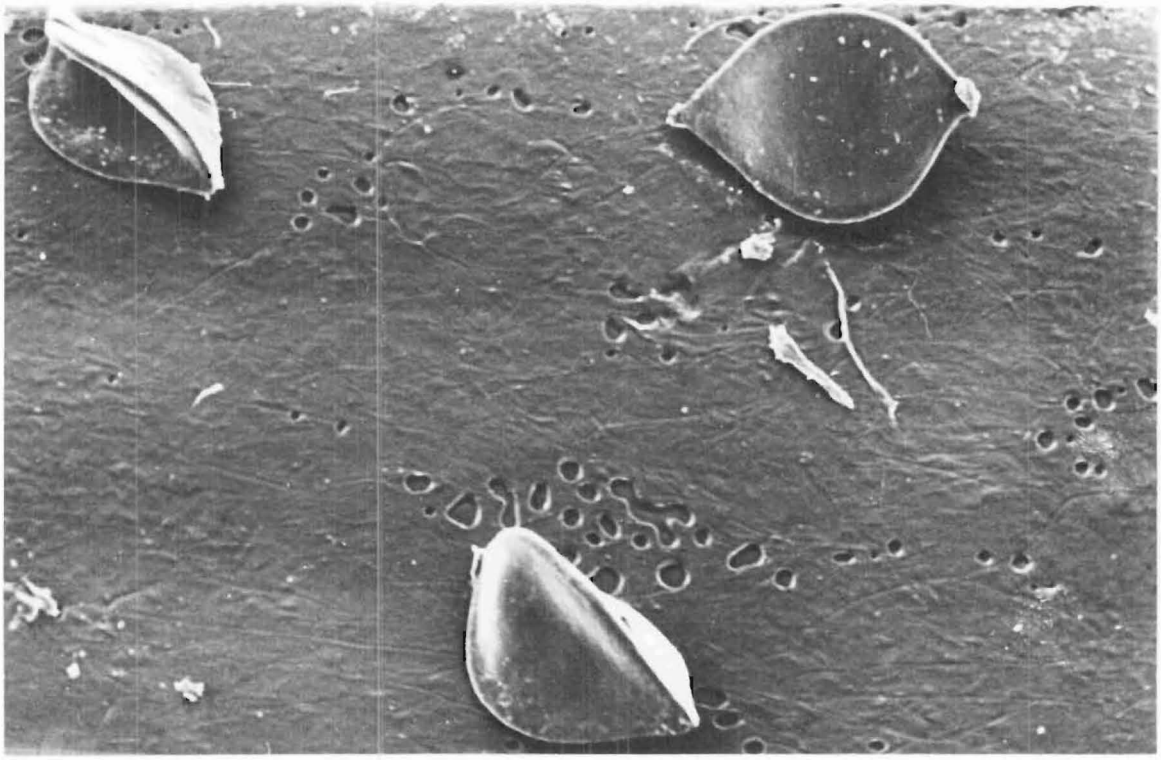
Mature *R. crispus* and *R. obtusifolius* seeds were collected from five plants at Plot 2 and Plot 5 respectively. The seed of each species was bulked, and five lots of 50 seeds were tested for percentage germination.

(3) Comparison of Weights and Germination Percentages of Seed from Primary and Secondary Branches of the Panicle

This experiment was designed to compare seeds borne on the main and secondary branches of *R. crispus* and *R. obtusifolius* plants. The specific object was to determine how much of the intermittent germination behaviour exhibited by the seeds of both species could be explained in terms of their different developmental environments.

The seeds borne on the main and secondary branches of four *R. crispus* and four *R. obtusifolius* plants were collected and kept separately to avoid masking any biologically significant features by the use of bulk samples (Salisbury 1965; Cavers and Harper 1966). The seeds were kept in dry storage for 16 weeks before the experiment. From each of these samples 50 seeds in their perianth segments were counted and weighed. The perianth segments were removed and the seeds reweighed. Each sample of 50 seeds was then germinated separately using the technique described under germination methods at a mean temperature of 25°C. This experiment was then repeated with a mean temperature 5°C lower. Results were recorded from the ninth to the fourteenth day, after which no further germination

Plate 5. *R. crispus* seeds (fruit without valves). The two seeds on the left show incomplete development compared to the normal seed on the right. (× 17).



took place in either experiment.

(4) The Proportion of Inviable Seeds on the Primary and Secondary Branches of the Panicles and their Effect on Germination Percentages

The seeds were drawn from the same source as those used to compare germination of seeds on the main and secondary branches of the panicle. From each group of seeds borne on the main and secondary branches five lots of 50 seeds were randomly selected. The seeds of each group were manually removed from their enclosing perianth segments and inspected. The absence of seed or shrivelled seed with concave rather than convex faces was scored for each sample (Plate 5). The remaining seeds were then tested for germination characteristics.

V. SEED DISPERSAL

(1) Dispersal of Seeds by Wind

To measure the relative distance that the seeds of *R. acetosella*, *R. crispus* and *R. obtusifolius* are dispersed by wind, a wind tunnel was set up. A trough 1.5 metres in length with a grid of 5 centimetre squares on its base was constructed. A fan at one end passed air through a 'honey-comb' which smoothed the flow of air along the trough. A shoot was placed just above the fan at an angle of 45° with one end in the air stream. The fan was located 25 centimetres above the base of the trough so that there was a layer of still air just above the grid. Seeds were placed in the shoot, which was then vibrated so that individual seeds were dropped into the air stream.

The seeds were carried along by the air stream until they fell into the layer of still air just above the grid. The fan speed was adjusted so that the maximum distance travelled by any seed was about one metre. The number of seeds in each five centimetre band from the fan was recorded.

One hundred seeds plus perianth segments of each species as well as an additional 100 seeds without perianth segments of both *R. crispus* and *R. obtusifolius* were tested.

(2) Dispersal of Seeds by Water

A hundred seeds of each species were chosen from the seeds used to establish the nursery populations. These were divided into five groups of twenty seeds each. Each group was placed in a 250 mℓ flask containing 100 mℓ of distilled water and the number of seeds which remained floating counted immediately. The flasks were then placed in a mechanical shaker and agitated for ten minutes, and the number of seeds still floating was counted again. The number of seeds which remained floating after ten minutes of agitation was recorded each day for a period of seven days. The mean number floating in the five flasks for each species was calculated for each period.

(3) Germination of Submerged Seeds

For each of the three species, 100 seeds were placed into each of five 250 mℓ flasks of distilled water. The flasks were shaken and exposed to a 16 hour day and alternating temperatures for fourteen days, after which the number of seeds which showed signs of germination in each flask was counted.

(4) The Gross Morphology of Seeds and the Abscission Zone and the Internal Structure of the Abscission Zone

Scanning electron micrographs were used to study the gross morphology of seeds and their enclosing perianth segments and the abscission zone. All samples were air dried and coated with gold-palladium.

The morphological changes in the abscission zones of *R. crispus* and *R. obtusifolius* were observed by making serial sections through the abscission zone of a number of peduncles of various ages and staining the sections with safranin and fast green.

Samples were taken from the same plant on four dates between January and July for both species. Direct comparisons between the species were not possible because they were at different developmental stages. Sampling dates were: 17 Jan, 14 March, 3 May and 10 July 1975.

VI. AGRICULTURAL EXPERIMENTS

(1) The Viability of *R. crispus* and *R. obtusifolius* Seeds at Various Stages of Maturity

This experiment was designed to determine the earliest stage of seed development at which a panicle could be cut and still develop viable seed.

A panicle was cut from each of 30 *R. crispus* and *R. obtusifolius* plants. The 30 panicles for each species were divided into groups according to whether they bore flowers, green seed or brown seed. These categories were chosen rather than days after anthesis as used by Maun (1974A) because although they are less accurate, they

are more easily distinguished under field conditions, the conditions which are most relevant in an agricultural context.

The cut panicles were stored in bundles in a garden shelter for three months and in conditions similar to those experienced by severed dock panicles after being mown and left on the field during the relatively dry summer months. The humidity under the experimental conditions was low.

From each group, five reproductive panicles which best represented the group were selected, and from each 50 flowers or seeds at a similar stage of maturity were counted and germinated under the conditions outlined in seed germination.

For this experiment, the seeds were left in the perianth segments. This was because under natural conditions, the first three stages of flower or seed development would invariably remain in their perianth segments after being mown. Although it is possible that mowing would loosen some of the mature seeds from their perianth segments, seeds germinating under field conditions often do so while they are still encased (Cavers and Harper 1966). Furthermore, preliminary trials had shown that under the conditions to be used in the experiment, up to 82% germination could be achieved within 16 days, despite the low germination rates Cavers and Harper (1966) obtained with seeds still encased in their perianth segments.

Thus for each species there were three stages of flower or seed maturity, each being represented by 50 buds, flowers or seeds with their perianth segments from five reproductive panicles (each from a separate plant).

(2) The Ability of *R. crispus* and *R. obtusifolius* Plants to Regenerate from Root Fragments

To establish whether or not dock plants are able to regenerate from root cuttings under conditions similar to those prevailing in the field plots and on local farms, the following experiment was carried out.

Ten plants each of *R. crispus* and *R. obtusifolius* were removed from every plot and the roots divided into five equal lengths. These were planted in shallow boxes containing fertilized soil.

The experiments were discontinued about three weeks after the top portion of most roots had shown vigorous regeneration.

CHAPTER IV

RESULTS

I. THE PHYSICAL CHARACTERISTICS OF THE SOIL AT EACH PLOT

The results of physical tests on the soil at each plot are presented in Table 2. The results of a principal components analysis indicated that the three principal components accounted respectively for 80, 18 and 3 per cent of the variation. A graph of each soil attribute against vector 1 showed that conductivity accounted for most of the differences between the soils at each plot (Fig. 1). Water holding capacity and water table level were the next most important variables followed by the percentage of organic content. Little variation between plots was accounted for by pH.

A graph of the most important variables is shown in Figure 2. Figs 2 & 3 suggest that the plots can be arranged so that their major soil differences vary linearly, in the order: 3, 4, 5, 1 and 6 (at the same site), 7, 8 and 9 (at the same site) and 2.

Table 2. PHYSICAL CHARACTERISTICS OF THE SOIL AT EACH PLOT

Plot	Water table	Water holding capacity (mℓ water/20 g soil)	pH	Conductivity	Per cent organic content
3	-4.0 m	7.46	5.34	319 **	4.75 *
4	-2.6 m	5.95	6.08	427 *	4.75 *
5	-0.6 m	9.14	7.26	555	4.72
1 & 6	0.0 m	17.02 *	5.52	1210 *	4.53
7,8 & 9	-1.0 m	16.18 *	5.52	1550	4.23 *
2	-0.2 m	18.02	7.54	1960	4.12

Lines connect pairs of results between which there are no significant differences.

(* = $P > 0.05$, ** = $P > 0.01$).

The figures for water holding capacity and pH are the means of three subsamples from each of five soil samples per plot. The figure for conductivity is the mean of five soil samples per plot.

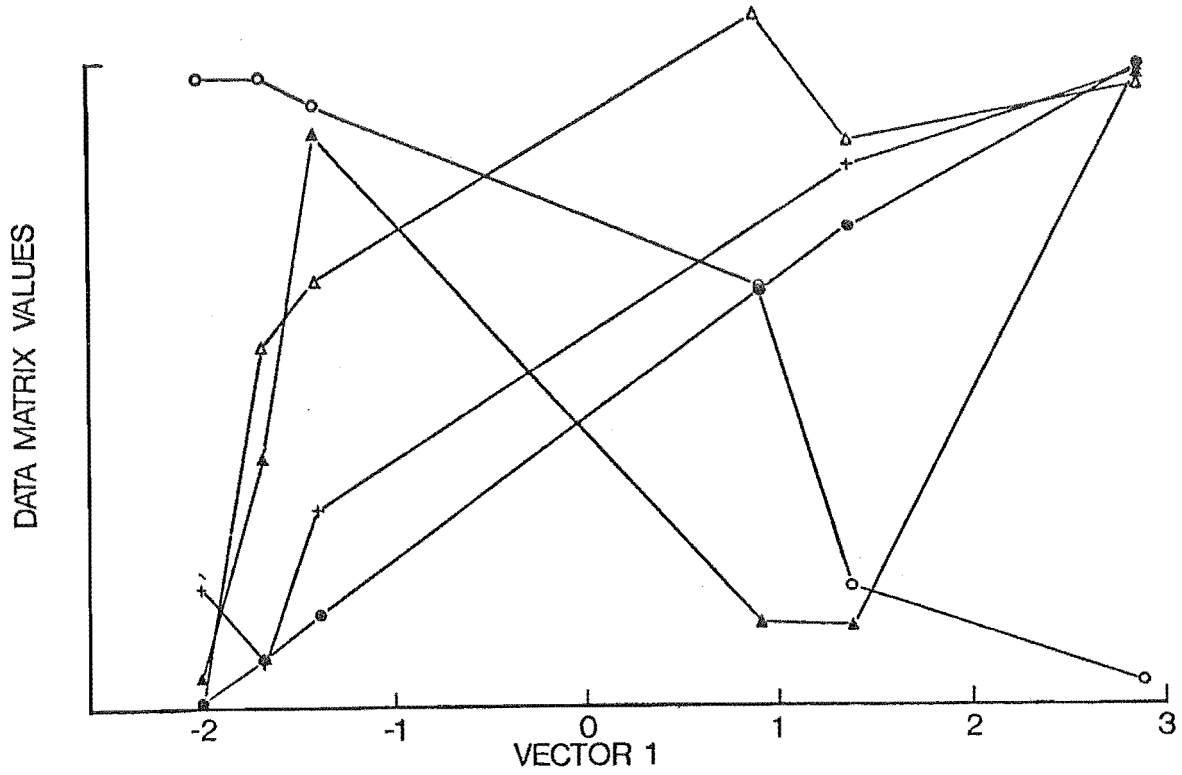


Fig. 1. Graph showing the relationship between vector 1 and the physical characteristics of the soil at each plot. Conductivity (●), per cent organic content (o), pH (▲), water holding capacity (+) and water table (△).

Data matrix values have been taken directly from Table 2.

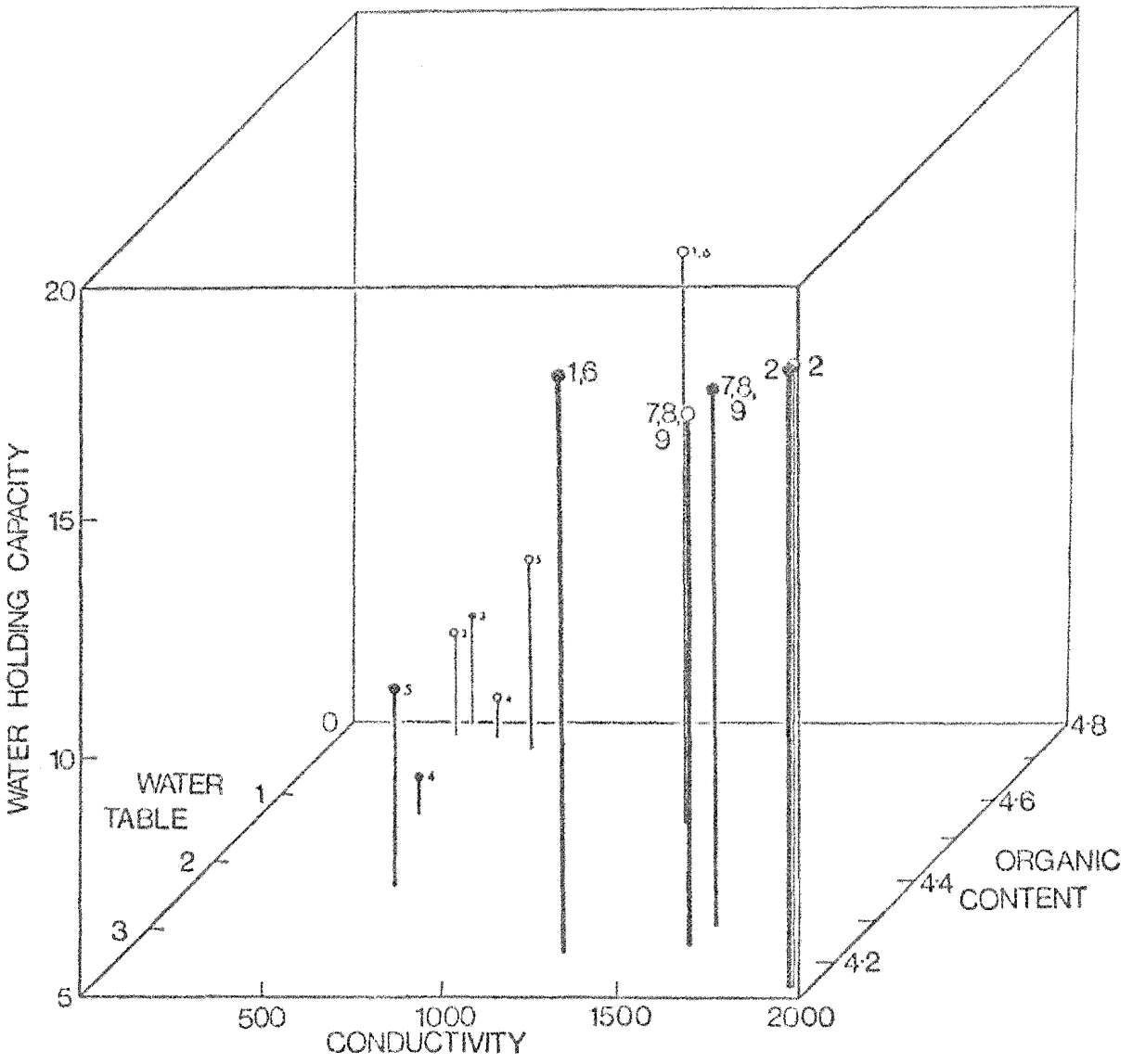


Fig. 2. The physical characteristics of the soil at each plot. Per cent organic content (o) and water table (●), (relative values).

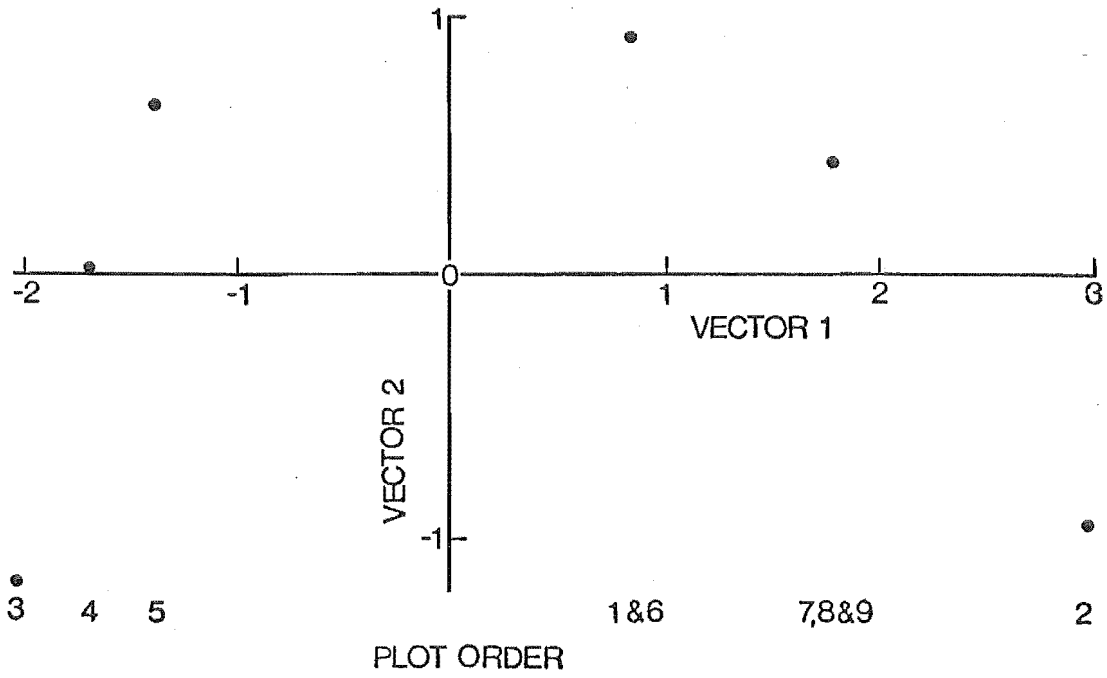


Fig. 3. Vector 1 plotted against vector 2 showing plot groupings.

II. LIFE HISTORY AND SURVIVORSHIP DATA

The population dynamics data are divided into two parts. The first part deals with plants past the seedling stage with at least two well developed leaves, and are referred to as "established" plants. The second part is concerned with seedlings.

The population dynamics data for *R. acetosella* treats each ramet rather than the genotype as an individual "plant". Apart from the practical necessity of regarding single vegetative offspring as separate "plants", the results of ^{14}C tracer studies presented below indicated that vegetative offspring behave as ecologically independent units.

(1) Changes in Population Size of Established Plants at Each Plot

(a) *R. acetosella* at plots 3 and 4: Net population numbers underwent large seasonal variations in plots 3 and 4 but tended to return to the same level at the same time of year (Figs 4 and 5). At a single survey carried out in November 1976, the population number was similar to that of previous years at plot 4, but about 10% lower at plot 3. Seasonal additions to the population were spread over a longer period in plot 3 than in plot 4, but in both plots additions tended to be greatest in the early summer months. Population losses were spread out evenly over the year except for a high initial loss at plot 3 after the first survey.

(b) *R. crispus* at plots 1 and 2: The changes in population numbers at these plots were not noticeably

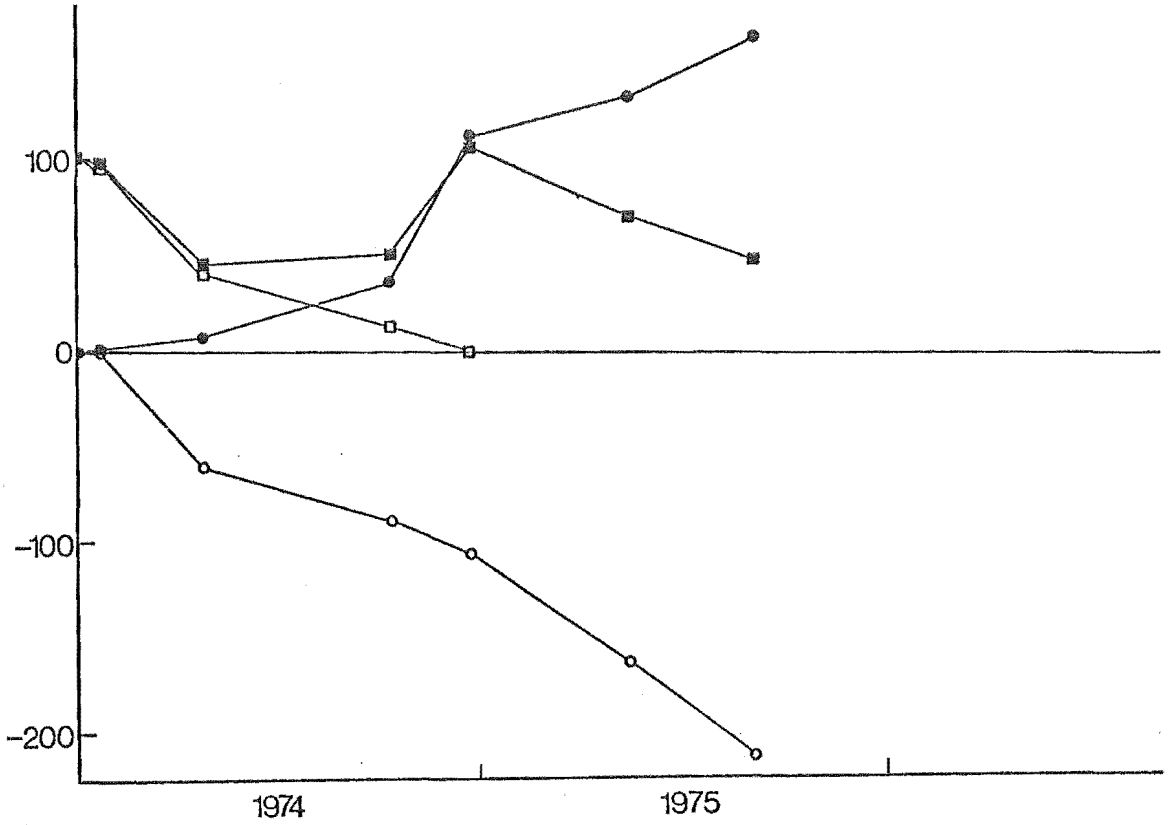


Fig. 4. Changes in population size of *R. acetosella* at plot 3. Net population size (■), cumulative gains (●), cumulative losses (o), survivorship of plants present in first survey (□).

Survey dates, Plot 3:

1 March, 23 March, 24 June, 11 December, 1974.

21 February, 12 July, 1 November, 1975.

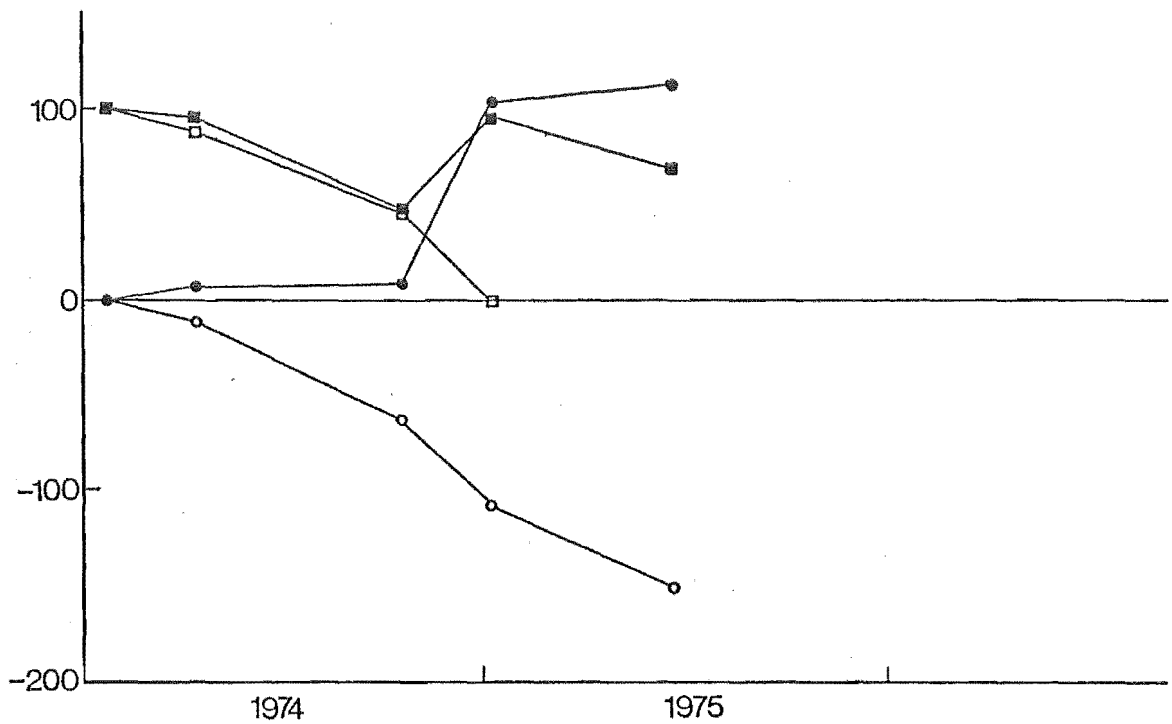


Fig. 5. Changes in population size of *R. acetosella* at plot 4. Net population size (■), cumulative gains (●), cumulative losses (o), survivorship of plants present in first survey (□).

Survey dates, Plot 4:

23 March, 10 June, 14 December, 1974.

9 March, 16 August, 1975.

seasonal. However, the survey frequency was not sufficiently high to detect any slight seasonal patterns of recruitment and mortality which may have been present.

The overall changes in population numbers at plot 1 were small compared to those which occurred in the *R. acetosella* populations. A slight increase in the population size over the first nine months was followed by a rapid decline in population numbers for the remainder of the study (Fig. 6). This decline was principally due to increasing mortality in the plants which had been present at the first survey, and the low rate of recruitment to the population. It was not possible to survey this plot in the last half of 1976 as the land was being used for other purposes.

Changes at plot 2 (Fig. 7) were much greater than at plot 1. Again no seasonal component was evident in these changes although additions to the population were slightly greater towards the end of both 1974 and 1976. After an initial increase, net population size declined until the end of the study. Both additions to and losses from the population were greater than at plot 1. Losses from the population were greater among younger plants than among older plants which had been present at the first survey.

(c) *R. obtusifolius* at plots 5 and 6: Changes in the *R. obtusifolius* population at plot 5 (Fig. 8) were similar to those of *R. crispus* at plot 2. A slight seasonal increase in the rate of recruitment to the population at plot 5 occurred towards the end of the last half of 1974 and 1976. Losses from the population were not seasonal. Net population size

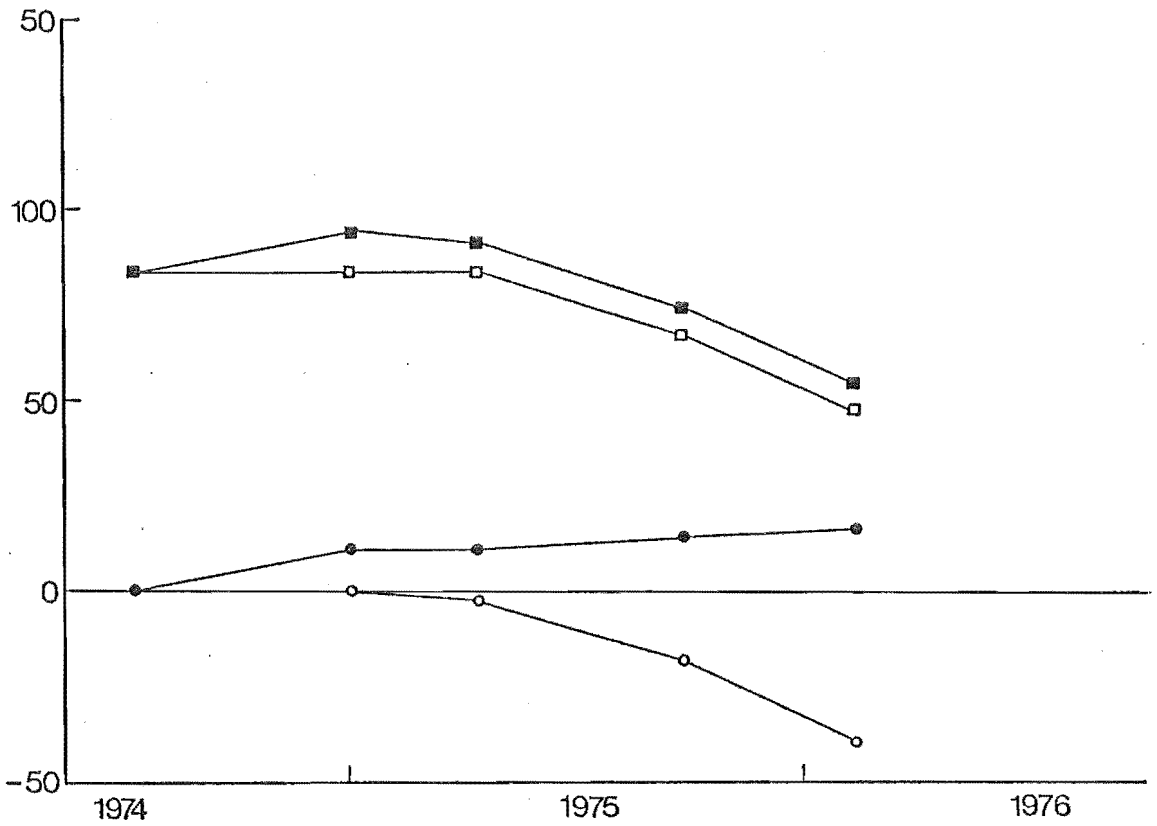


Fig. 6. Changes in population size of *R. crispus* at plot 1. Net population size (■), cumulative gains (●), cumulative losses (o), survivorship of plants present in first survey (□).

Survey dates, Plot 1:

6 May, 15 November, 1974.

10 March, 11 September, 1975.

29 February, 1976.

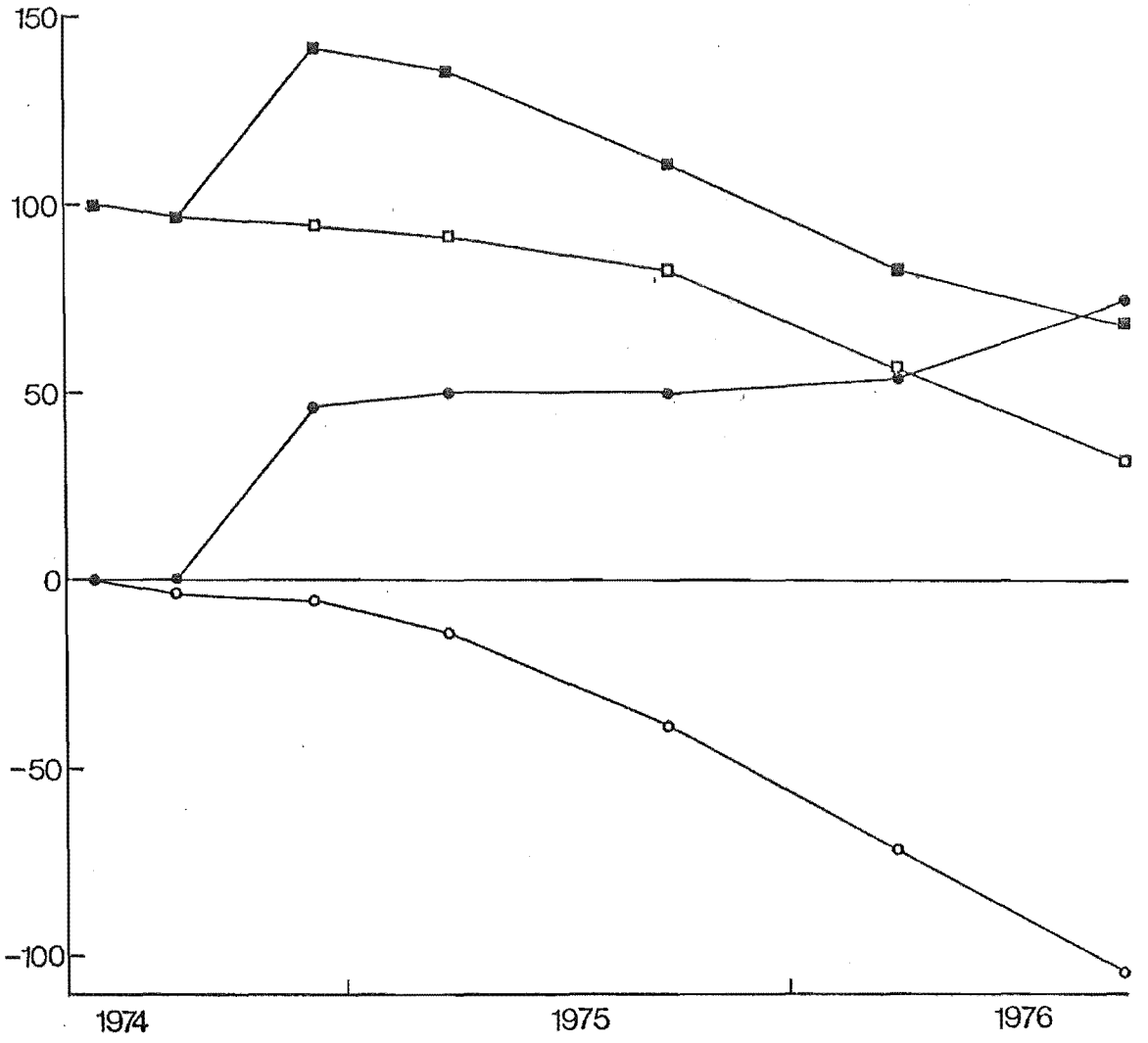


Fig. 7. Changes in population size of *R. crispus* at plot 2. Net population size (■), cumulative gains (●), cumulative losses (o), survivorship of plants present in first survey (□).

Survey dates, Plot 2:

28 March, 7 June, 16 October, 1974.

20 February, 9 September, 10 April, 1975.

4 November, 1976.

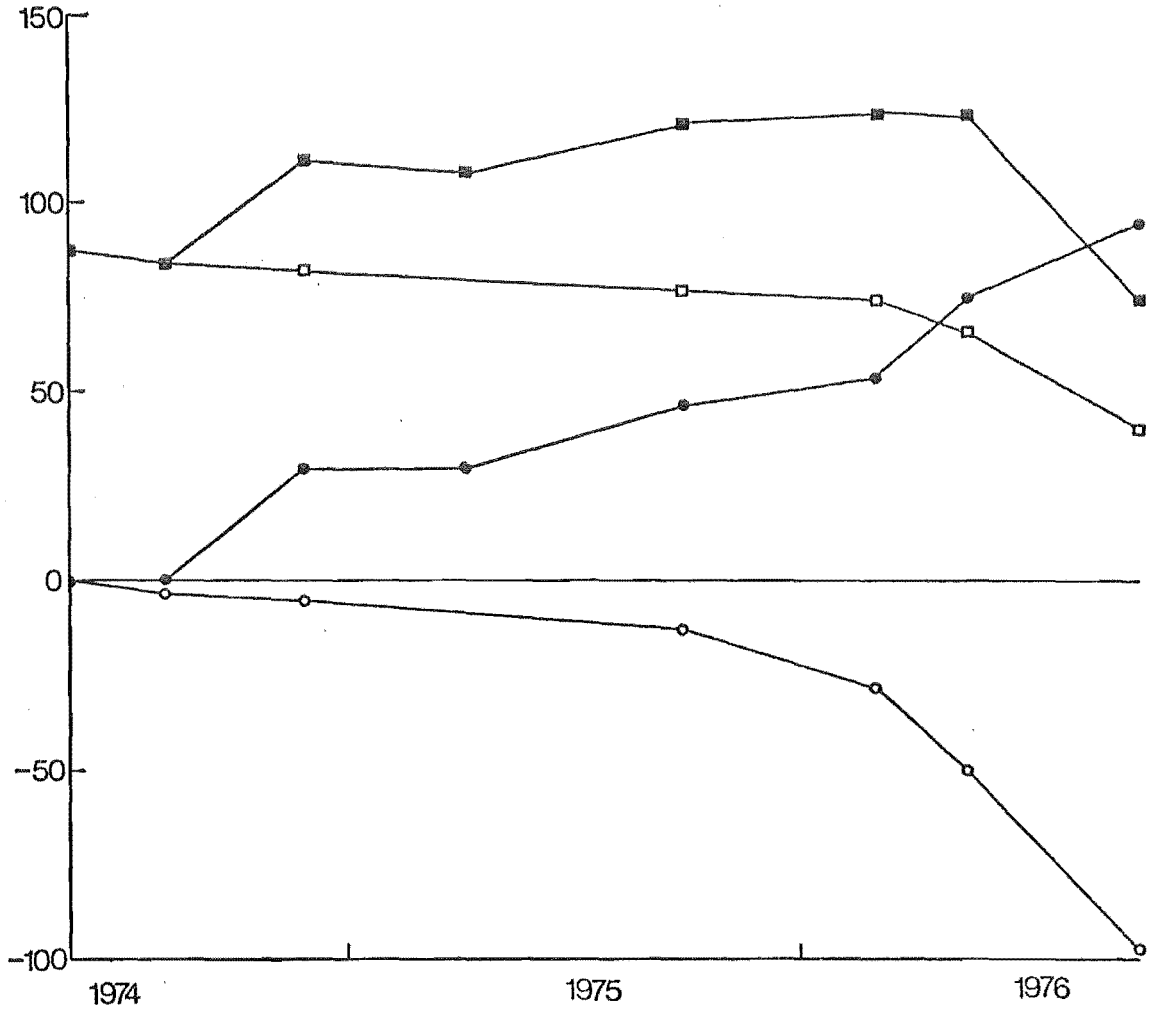


Fig. 8. Changes in population size of *R. obtusifolius* at plot 5. Net population size (■), cumulative gains (●), cumulative losses (o), survivorship of plants present in first survey (□).

Survey dates, Plot 5:

2 March, 24 May, 6 October, 1974.

13 February, 15 September, 1975.

10 March, 28 May, 4 November, 1976.

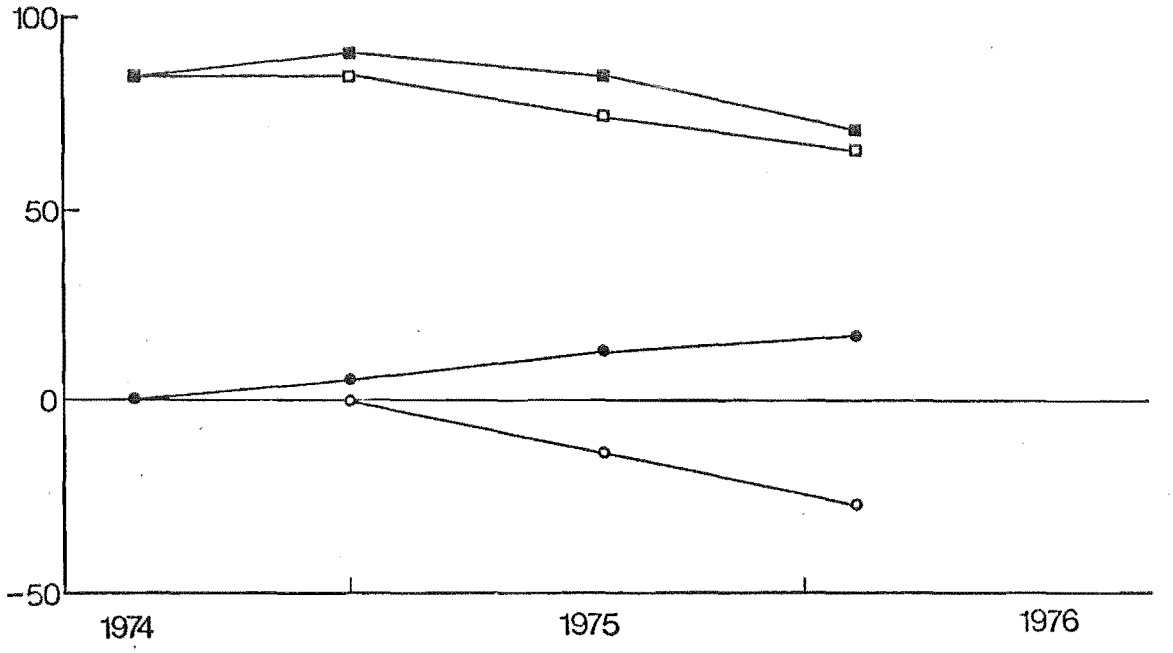


Fig. 9. Changes in population size of *R. obtusifolius* at plot 6. Net population size (■), cumulative gains (●), cumulative losses (○), survivorship of plants present at first survey (□).

Survey dates, Plot 6:

6 May, 15 November, 1974.

3 July, 12 December, 1975.

increased until the beginning of January 1976 after which time it dropped sharply. Up to that time losses from the population were principally due to mortality amongst the plants present at the first survey. After January 1976, mortality in both the original population and plants recruited to the population since the first survey increased.

Changes in population numbers of *R. obtusifolius* plants at plot 6 (Fig. 9) were similar to those of the *R. crispus* population at the same site in plot 1 and also showed no seasonal variation. Overall, the net population declined slightly during the period of the survey.

The population dynamics of the three species planted at the nursery site are not included in the results because of the very low mortality at this site during the period of study. At this site the *R. acetosella* population did not undergo the large seasonal fluctuations experienced in the two field plots.

(2) Population Flux of Established Plants

Population flux in each plot was measured by calculating the percentage survival of plants present at yearly intervals and for the total length of the study. This, and the percentage mortality for all plots, is shown in Tables 3, 4, 5 and 6. The turnover time for the whole period of study has been calculated by the formula:

$$\frac{\text{interval in years}}{\text{per cent mortality of plants present at the first survey}} \times 100$$

Half-life (the time for half the plants to die) has been estimated from the survivorship curve for plants at each plot (Fig. 10). Half lifes are strictly valid only for

Table 3. POPULATION FLUX IN *R. acetosella* PLANTS AT PLOTS 3 AND 4

	Plot 3	Plot 4
	Period Year 1	Period Year 1
a. No. of plants present at beginning of period	100	100
b. No. of plants present at end of period	105	103
c. Net change (b-a)	+ 5	+ 3
d. Rate of increase (b/a) for period	1.05	1.03
e. No. of plants gained during period	111	103
f. No. of plants lost during period	104	107
g. No. of plants present at beginning and end of period	0	0
h. Per cent survival of plants in (a) (g/a × 100)	0%	0%
i. Total plants recorded during period	211	203
j. Per cent mortality of all individuals for period (f/i × 100)	*	*

* All plants died within 1 year.

Overall measures do not indicate population trends in this seasonal species.

Table 4. POPULATION FLUX IN *R. crispus* PLANTS AT PLOTS 1 AND 2

*	PLOT 1			PLOT 2		
	Period			Period		
	Year 1	Remaining 287 days	Overall (652 days)	Year 1	Year 2	Overall (953 days)
a. Initial plant no.	84	87	84	100	130	100
b. Final plant no.	87	55	55	130	84	69
c. Net change	+3	-32	-29	+30	-46	-31
d. Rate of increase	1.0	0.6	0.7	1.3	0.6	0.7
e. No. plants gained	12	4	16	50	4	85
f. No. plants lost	9	33	40	19	51	104
g. No. persistent plants	80	50	49	90	43	32
h. Survival	95%	57%	58%	90%	33%	32%
i. Total plants	96	91	100	175	134	185
j. Mortality	9%	36%	40%	11%	38%	56%

* See Table 3 for detailed key.

Table 5. POPULATION FLUX IN *R. obtusifolius* PLANTS AT PLOT 5

*	Period			
	Year 1	Year 2	Remaining 252 days	Overall (980 days)
a. Initial plant no.	87	115	123	87
b. Final plant no.	115	123	74	74
c. Net change	+28	+8	-49	-13
d. Rate of increase	1.3	1.1	0.6	0.9
e. No. plants gained	37	16	37	94
f. No. plants lost	8	19	70	97
g. No. persistent plants	80	82	34	40
h. Survival	92%	71%	30%	46%
i. Total plants	124	131	152	181
j. Mortality	7%	15%	61%	54%

* See Table 3 for detailed key.

Table 6. POPULATION FLUX IN *R. obtusifolius* PLANTS AT PLOT 6

*	Period		
	Year 1	Remaining 287 days	Overall
a. Initial plant no.	85	83	85
b. Final plant no.	87	71	71
c. Net change	+2	-12	-14
d. Rate of increase	1.0	0.9	0.8
e. No. plants gained	11	5	16
f. No. plants lost	9	17	27
g. No. persistent plants	77	71	66
h. Survival	91%	85%	78%
i. Total plants	96	88	101
j. Mortality	9%	20%	27%

* See Table 3 for detailed key.

populations with completely linear survivorship curves. Although the survivorship curves presented here for *R. crispus* and *R. obtusifolius* are not linear in their latter portions, half life estimates have been made for comparative purposes.

Median turnover time measures the time taken for the number of survivors of the original population to equal the number of additions to the population. At the median turnover time, half of the existing population is made up of new individuals. Median turnover time rather than half life relates the rate of loss of the original population to the recruitment rate and hence changes in net population size. Median turnover time was estimated from the point of intersection of the survivorship curve of the plants present at the first survey and the cumulative recruitment curve for each plot. This was done by extrapolation for two plots.

The ratio of net population size at the end and beginning of the median turnover time for the *R. crispus* and *R. obtusifolius* plots at the same site were the same, indicating that the overall rate of population decline at plots 1 and 6 were similar. The other *R. obtusifolius* population showed a slight increase which was reversed after the median turnover time.

Although median turnover times for *R. crispus* plants were slightly shorter than those for *R. obtusifolius* plants, the differences between plots for each species were as great as the differences between species. A measure of the ratio of net population size at the beginning and end of this interval indicates the overall trend in population numbers. Turnover time, half-life and median turnover time measures

Table 7: SUMMARY OF POPULATION FLUX MEASURES

Species	Plot No.	Turnover time	Half-life	Median turnover time	Rate of increase to median turnover time. *
R. acetosella	3	1	0.6	-	-
R. acetosella	4	1	0.7	-	-
R. crispus	1	4.2	1.9	2.7	0.37
R. crispus	2	3.8	2.1	2.1	0.82
R. obtusifolius	5	5.0	2.7	2.2	1.23
R. obtusifolius	6	5.2	2.1	3.6	0.37

All time measures recorded in years.

* Interval measured from beginning of observations to median turnover time.

are presented in Table 7. Median turnover time is less informative for species with synchronized behaviour of the individuals, and consequently is not shown for the two *R. acetosella* plots.

(3) Survivorship of Established Plants

Tables 8, 9, 10, 11, 12 and 13 summarize information about the numbers and times of death of all plants which were recorded at the initial and subsequent surveys at all plots. The survivorship curves of the plants present at the first survey conducted in each plot are shown in Fig. 10. The time scale represents minimum age because the length of time for which plants were present before the first survey was not known. However, the seasonal death of nearly all *R. acetosella* "plants", and the time of year of the first survey at plots 3 and 4, indicates that the average age of *R. acetosella* plants at the first survey was about four months. Thus the 1974 survivorship curve for this species plots the decline in the number of plants which were between the end and the middle of their lives. The curves for the other two species represent the survivorship of a comparatively wide range of plant ages, sizes and classes.

The survivorship curves for *R. crispus* and *R. obtusifolius* conformed to the exponential model for the first portion of the study but deviated from it markedly towards the end. This indicates that initially the established plants faced a constant probability of survival per unit time, but that towards the end of the study the probability of survival per unit time decreased markedly.

Table 8: SURVIVORSHIP DATA FOR *R. acetosella* PLANTS AT PLOT 3

Survey number	1	2	3	4	5	6	7
Days after 1 March 1974	0	23	115	286	358	499	611
No. of plants	100	97	40	12	0	-	-
"		1	1	1	1	1	1
"			7	6	5	2	0
"				28	25	15	3
"					75	31	9
"						22	10
Cumulative gains		1	8	36	111	133	163
Cumulative losses		3	60	89	105	162	211
Net population	100	98	48	47	106	71	52

Table 9: SURVIVORSHIP DATA FOR *R. acetosella* PLANTS AT PLOT 4

Survey number	1	2	3	4	5
Days after 1 March 1974	22	102	289	374	534
No. of plants	100	88	45	0	-
"		7	1	0	-
"			1	1	0
"				95	59
"					9
Cumulative gains		7	8	103	112
Cumulative losses		12	63	107	142
Net population	100	95	47	96	68

Table 10. SURVIVORSHIP DATA FOR *R. crispus* PLANTS AT PLOT 1

Survey number	1	2	3	4	5
Days after 1 March 1974	66	260	375	560	731
No. of plants	84	84	84	68	49
"		11	9	9	7
"			-	-	-
"				3	2
"					2
Cumulative gains		11	11	14	16
Cumulative losses		0	2	18	40
Net population	84	95	92	75	60

Table 11. SURVIVORSHIP DATA FOR *R. crispus* PLANTS AT PLOT 2

Survey number	1	2	3	4	5	6	7
Days after 1 March 1974	27	99	230	357	558	772	980
No. of plants	100	97	95	92	83	57	32
"		-	-	-	-	-	-
"			47	41	26	20	12
"				3	2	2	2
"					-	-	-
"						4	2
"							21
Cumulative gains		0	47	50	50	54	75
Cumulative losses		3	5	14	39	71	104
Net population	100	97	142	136	111	83	69

Table 12. SURVIVORSHIP DATA FOR *R. obtusifolius* PLANTS AT PLOT 5

Survey number	1	2	3	4	5	6	7	8
Days after 1 March 1974	1	85	220	350	564	741	820	980
No. of plants	87	84	82	80	77	74	65	40
"		-	-	-	-	-	-	-
"			30	28	27	21	17	12
"				-	-	-	-	-
"					17	11	9	2
"						17	10	5
"							21	16
"								19
Cumulative gains		0	30	30	47	54	75	94
Cumulative losses		3	5	9	13	28	50	97
Net population	87	84	112	108	121	123	122	94

Table 13. SURVIVORSHIP DATA FOR *R. obtusifolius* PLANTS AT PLOT 6

Survey number	1	2	3	4
Days after 1 March 1974	66	260	490	652
No. of plants	85	85	75	66
"		6	3	2
"			7	3
"				3
Cumulative gains		6	13	16
Cumulative losses		0	13	27
Net population	85	91	85	71

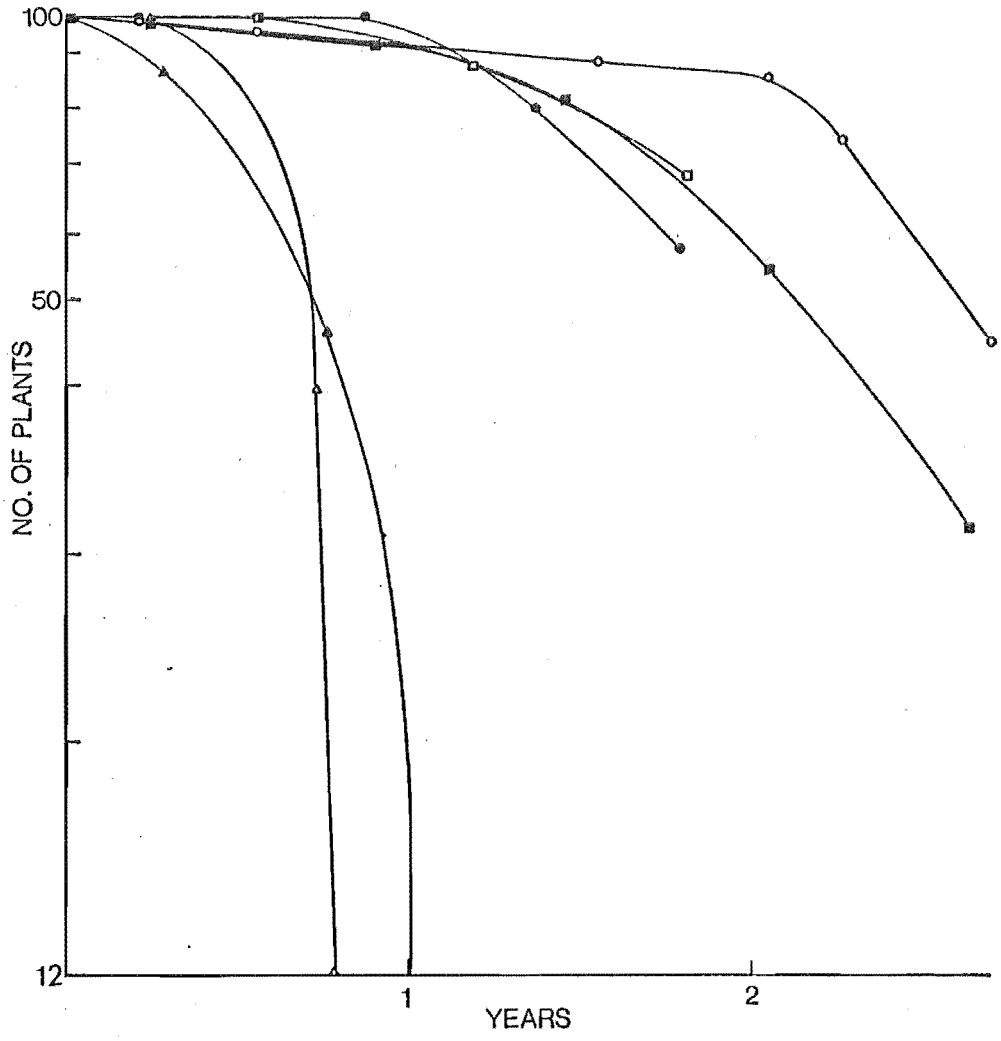


Fig. 10. Survivorship of plants at each plot.
R. acetosella, plot 3 (△), plot 4 (▲). *R. crispus*, plot 1 (●), plot 2 (■). *R. obtusifolius*, plot 5 (o), plot 6 (□).
The time scale measures the minimum age of plants.

(4) The Probability of Survival for Established Plants at Successive Intervals

The probability of survival was calculated at each survey for the plants present in the first survey. The results for all plots are shown in Figs 11, 12 and 13, the curves showing survival rates at successive intervals after the first survey. Points represent the probability of survival in the 100 days before the survey.

Because all *R. acetosella* "plants" died each year, it was possible to calculate survival rates for two different groups of plants at each plot. The curve for plot 3 in 1974 shows a low probability of survival in the early stages, and is not typical of the survival rate data for the next year, or at the other *R. acetosella* plot.

The probability of survival curves for *R. acetosella* represent the probability of survival for vegetatively produced "plants" which are in the latter parts of their growth cycle. These show a rapidly decreasing probability of survival, reaching 0.0% within a year. The survival rate curves for the other two species cover a larger portion of the life cycle. In plots 2 and 5 (Figs 12 and 13) both the *R. crispus* and *R. obtusifolius* plants initially had a high, increasing probability of survival. This was followed by a period with a relatively constant probability of survival until the end of the second year. After this the probability of survival decreased to one seventh and one tenth that in the previous two years, for *R. crispus* and *R. obtusifolius* respectively.

At plots 1 and 6 (Figs 12 and 13) a period with a high probability of survival was followed by a decrease in

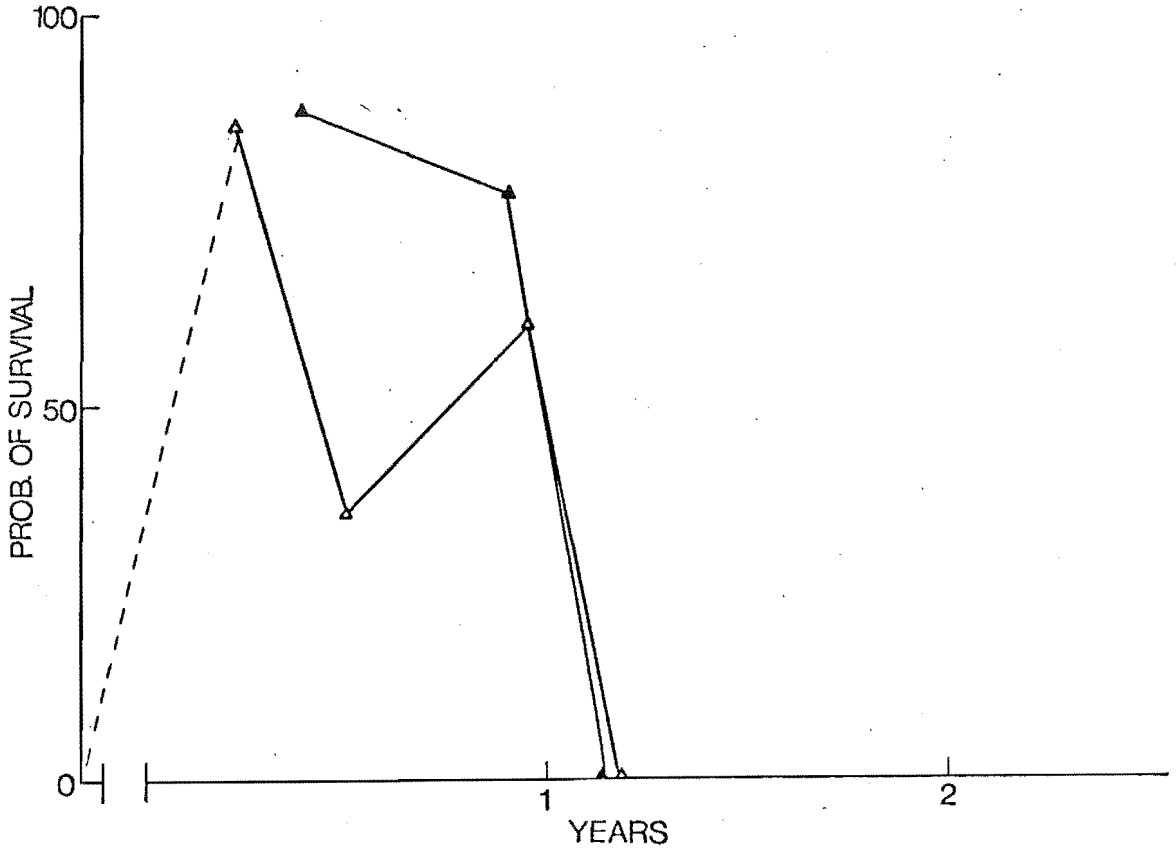


Fig. 11. Survival rate per 100 R.acetosella plants. Plot 3 (△), plot 4 (▲).

Survival of vegetatively produced plants (——). Survival of seedlings (----).

The survival rate per 100 plants for the 100 days previous to each survey was calculated from the following formula for Figs. 11, 12, and 13:

$$N(n) - \frac{100(N(n) - N(n+1))}{d} \cdot \frac{100}{N(n)}$$

where N = the number of plants present at survey n, and d is the interval between survey n and n+1 in days.

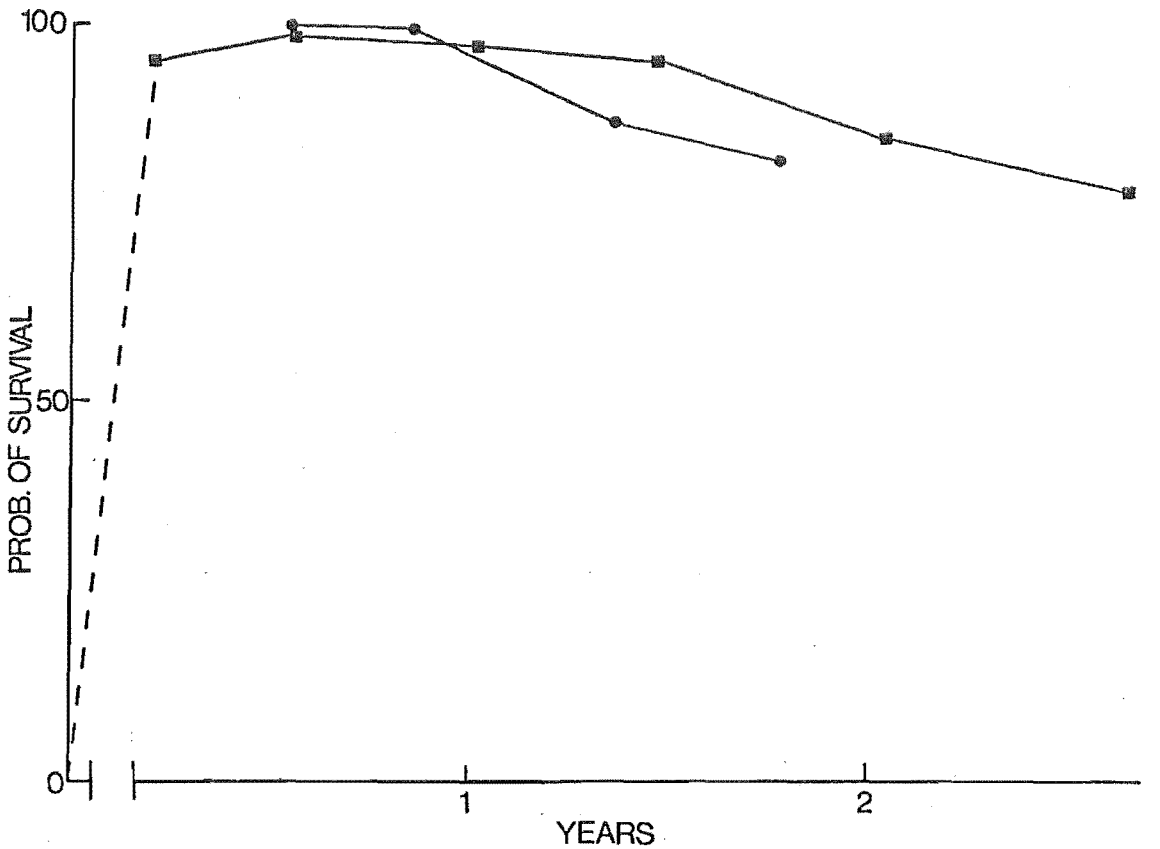


Fig. 12. Survival rate per 100 *R. crispus* plants. Plot 1 (●), plot 2 (■). Time scale shows minimum age. Survival rate of seedlings shown by (---).

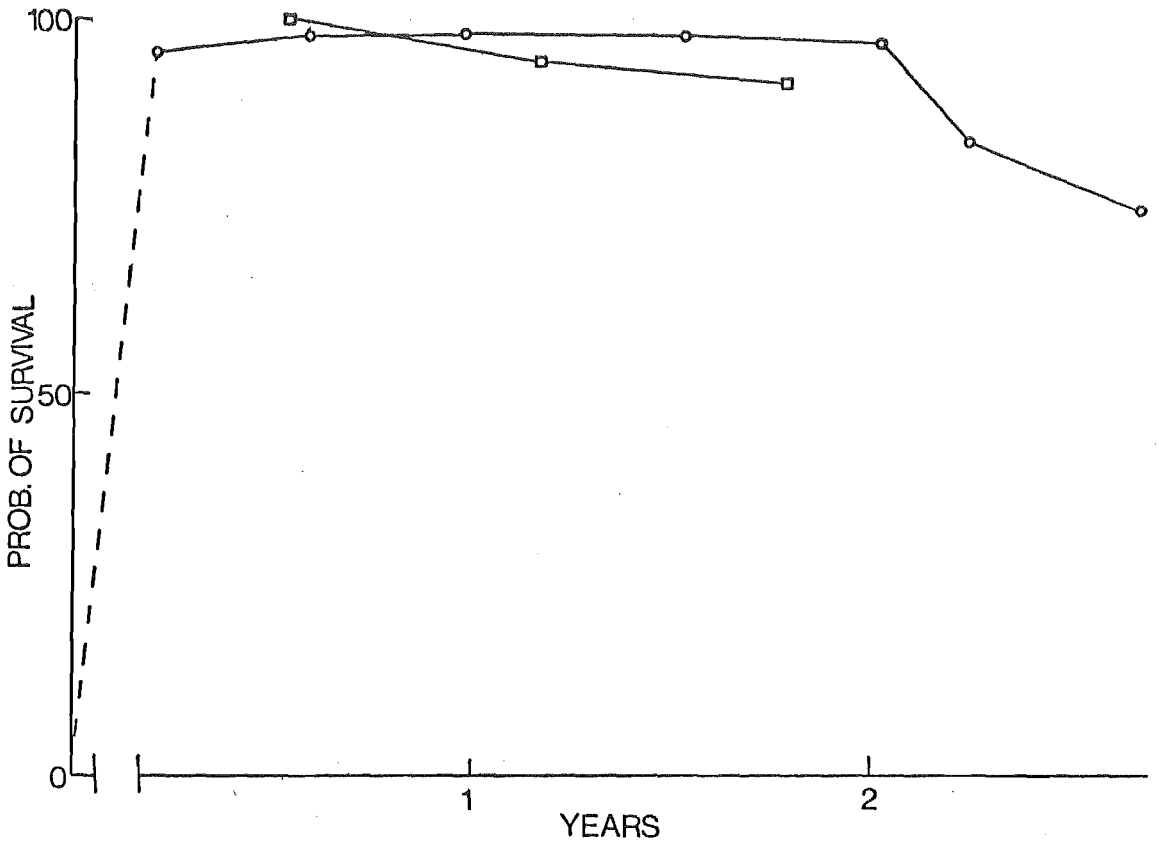


Fig. 13. Survival rate per 100 *R. obtusifolius* plants. Plot 5 (o), plot 6 (□). Time scale shows minimum age. Survival rate of seedlings shown by (---).

the probability of survival.

The period of observations at these two plots were restricted in length, and the changing trends in the probability of survival after two years could not be determined.

(5) The Proportion and Mortality of Post-flowering and Non-flowering Plants

The term "post-flowering" is used to denote plants which had flowered previously or were flowering at the survey under consideration. "Non-flowering" plants denotes plants which had not flowered by the time of the survey under consideration.

The proportion of non-flowering plants at each survey is plotted in Figs 14, 15 and 16 for the original population at each plot. The proportion of plants which had flowered increased with time at all plots.

The low number of post-flowering plants in early surveys at the two *R. acetosella* plots reflects the seasonal development of the plants. The low number of plants which had flowered in the first few surveys at the other plots was due to the early stage of development of some of the plants, and a slight underestimate of the number of plants which had flowered previously. This occurred because plants which had flowered and lost their reproductive panicles before the first survey would initially have been recorded as non-flowering.

The increase in the proportion of non-flowering plants at some surveys was due to higher mortality amongst post-flowering plants.

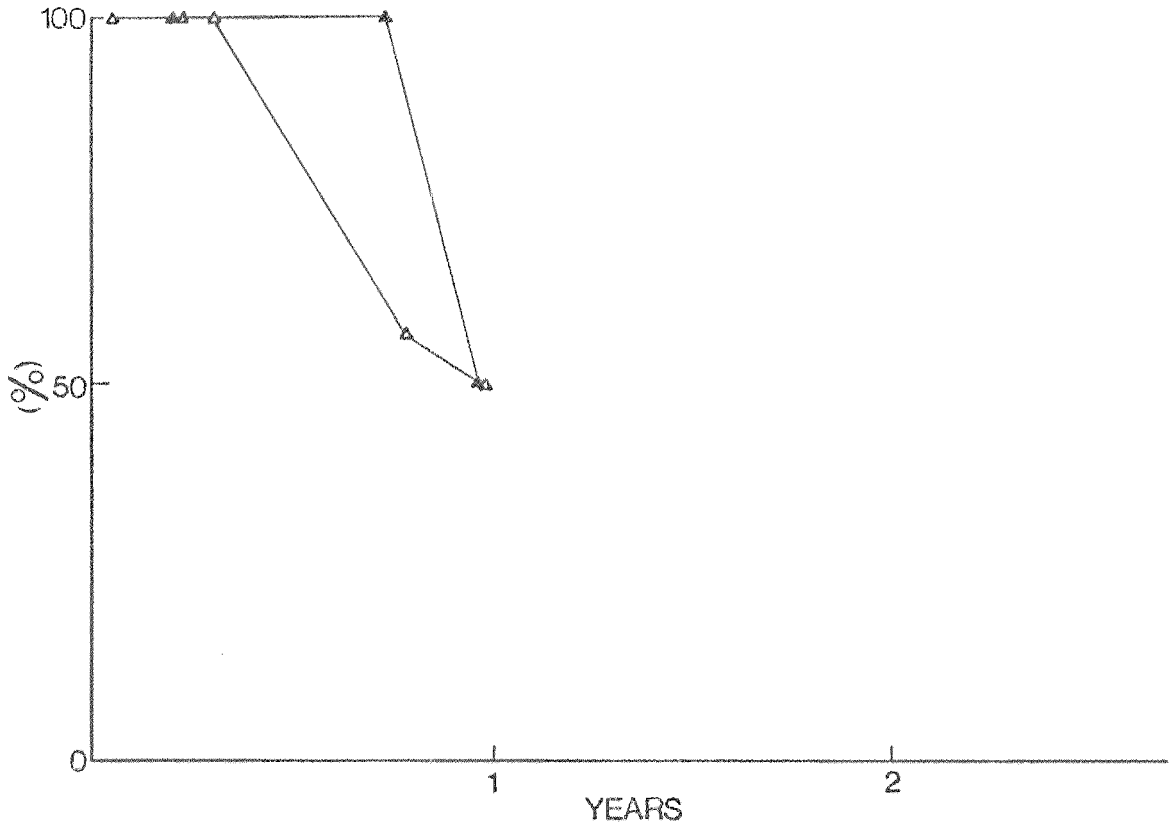


Fig. 14. Proportion (as a percentage) of *R. acetosella* plants in non-flowering classes at successive surveys. Plot 3 (Δ), plot 4 (▲).

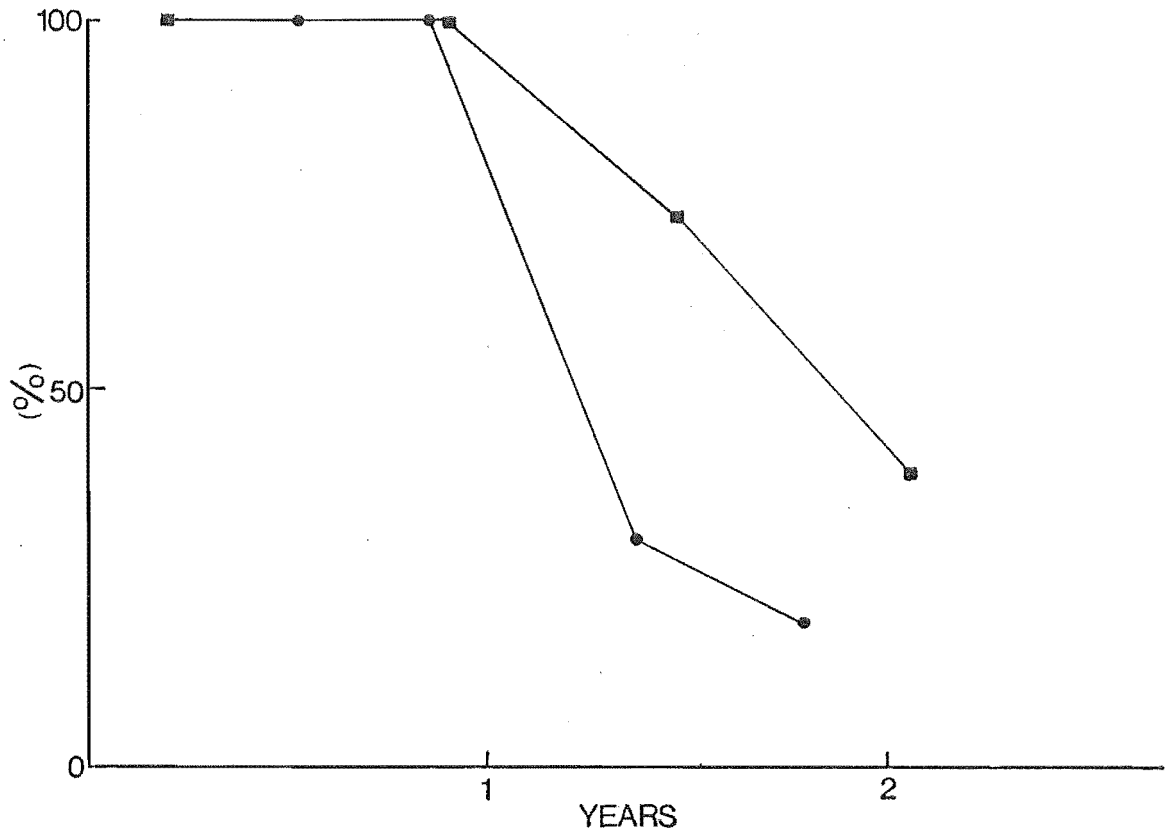


Fig. 15. Proportion (as a percentage) of *R. crispus* plants in flowering and non-flowering classes at successive surveys. Plot 1 (●), plot 2 (■).

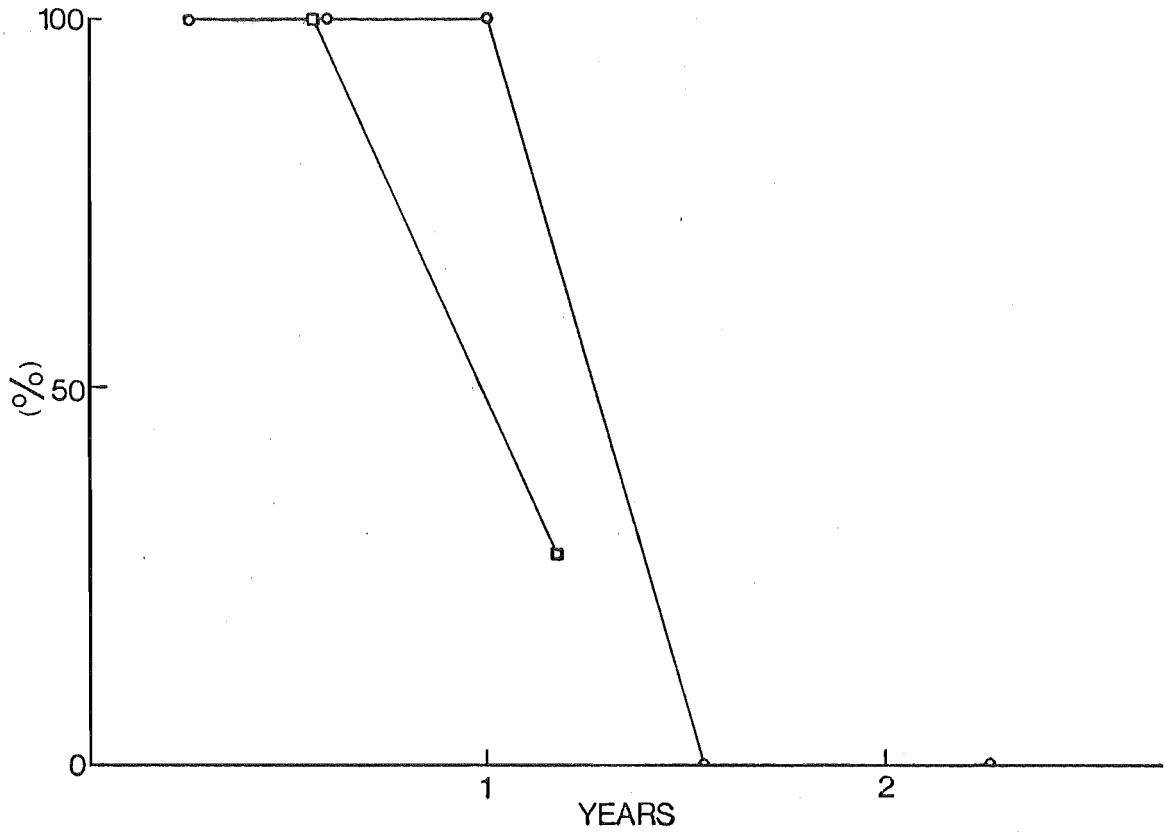


Fig. 16. Proportion (as a percentage) of *R. obtusifolius* plants in non-flowering classes at successive surveys. Plot 5 (o), plot 6 (□).

To measure the proportion of total mortality accounted for by post-flowering and non-flowering plants, the mortality rate for these two classes was calculated separately. The mortality rates for post-flowering and non-flowering plants are shown in Table 14 for the 100 days before each survey.

The mortality rate of non-flowering plants showed no consistent trend, whilst it increased markedly for post-flowering plants. The relative proportion of mortality in these two classes is shown in Figure 17.

That the increase in mortality amongst post-flowering *R. crispus* and *R. obtusifolius* was not an artefact due to deteriorating conditions is shown by the absence of a similar increase in mortality with time amongst plants which did not flower.

(6) The Mortality Rate in Male and Female *R. acetosella* Plants

In plot 3, 37 *R. acetosella* plants which survived to survey three had reproductive panicles at a stage which could be sexed. Amongst the females, twice as many died as survived to the following survey. The number of males which survived to the following survey equalled the number which did not. A Chi squared test showed that this difference was not significant, therefore there was only an inconclusive suggestion that females died earlier. ($\chi^2 = 3.8$, $p > 0.1$).

It was not possible to carry out similar measures at plot 4 because the surveys did not coincide with a period during which sufficient plants could be sexed.

Table 14. MORTALITY AMONGST POST-FLOWERING AND NON-FLOWERING PLANTS.

Species Plot No.	Interval 1 - 2	2 - 3	3 - 4	4 - 5	5 - 6	6 - 7
R. acetosella 3	NF $\frac{3}{100}$ = 3%	$\frac{57}{97}$ = 58.7%	$\frac{4}{5}$ = 80%	$\frac{1}{1}$ = 100%		
	F		$\frac{24}{35}$ = 69%	$\frac{8}{8}$ = 100%		
R. acetosella 4	NF $\frac{12}{100}$ = 12%	$\frac{43}{88}$ = 48.9%	$\frac{23}{23}$ = 100%			
	F		$\frac{22}{22}$ = 100%			
R. crispus 1	NF $\frac{0}{84}$ = 0%	$\frac{0}{84}$ = 0%	$\frac{1}{10}$ = 10%	$\frac{1}{8}$ = 12.5%		
	χ^2		0.121NS	0.005NS		
	F		$\frac{15}{74}$ = 20.3%	$\frac{18}{60}$ = 30%		
R. crispus 2	NF $\frac{3}{100}$ = 3%	$\frac{2}{97}$ = 2.1%	$\frac{3}{89}$ = 3.4%	$\frac{3}{20}$ = 15%	$\frac{4}{17}$ = 23.5%	
	χ^2			0.213NS	0.238NS	
	F		$\frac{0}{6}$ = 0%	$\frac{6}{72}$ = 8.3%	$\frac{22}{66}$ = 33.3%	$\frac{25}{57}$ = 43.9%
R. obtusifolius 5	NF $\frac{3}{87}$ = 3.4%	$\frac{2}{84}$ = 2.3%	$\frac{2}{82}$ = 2.4%	$\frac{0}{28}$ = 0%	$\frac{1}{28}$ = 3.6%	$\frac{0}{27}$ = 0%
	χ^2			0.034NS	0.233NS	4.3*
	F			$\frac{3}{52}$ = 5.8%	$\frac{2}{49}$ = 4.1%	$\frac{9}{47}$ = 19.1%
R. obtusifolius 6	NF $\frac{0}{85}$ = 0%	$\frac{10}{85}$ = 11.8%	$\frac{1}{25}$ = 4%			
	χ^2		1.200NS			
	F		$\frac{8}{50}$ = 16%			

NF = non-flowering plants, F = post-flowering plants.
The denominator of each fraction shows the number of plants present at the beginning of the interval, numerator the number dying by the end of the interval.
Percentages show the percent mortality for each interval.

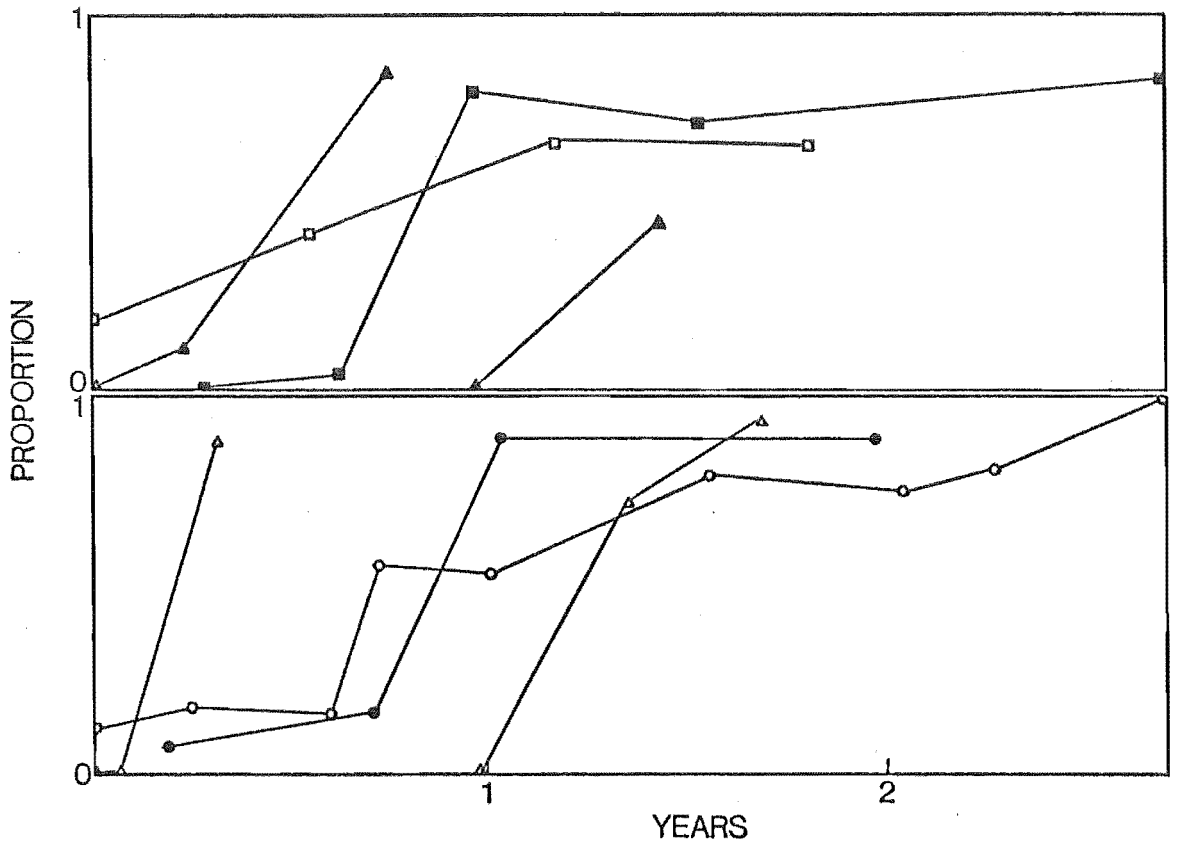


Fig. 17. Proportion of post-flowering plants amongst those which died at each survey.
R. acetosella, plot 3 (△), plot 4 (▲).
R. crispus, plot 1 (●), plot 2 (■).
R. obtusifolius, plot 5 (o), plot 6 (□).

(7) The Probability of Mortality for Seedlings

To estimate seedling mortality rates, the number of seeds which germinate must be compared to the number of plants which are recruited to the population of established plants per unit time.

In this study, three lots of samples were taken at each plot over a period of three months. Both the seedlings appearing and dying between sampling times and those appearing during the other nine months of the year have not been accounted for. Thus the numbers of seedlings recorded are minimum estimates. The minimum numbers of seedlings appearing per year in the area occupied by quadrats are recorded in Table 15.

Minimum estimates of per cent mortality did not fall below 98% of any plot. At plots 3 and 4, no additions to the populations from seed were observed, although it is probable that a small number did occur. At the site of plots 1 and 6 it was not possible to differentiate between *R. crispus* and *R. obtusifolius* seedlings. Thus, half the number of seedlings appearing per square metre have been used to calculate the mortality figures for each species. Because of the extremely low survival of seedlings at plots 1 and 6, mortality was recorded as 99+ per cent.

If an approximation of the time required for seedlings to reach an age at which they would be included in the major surveys is made, survival rates for seedlings can be calculated. On the basis of field observations a period of four weeks was used for *R. acetosella* seedlings and five weeks for the other two species. Seedling survival rates are shown in Figs 11, 12 and 13 as dashed lines.

TABLE 15. MORTALITY ESTIMATES FOR SEEDLINGS

Species	Plot No.	Number of seedlings appearing/m^2 from three samples. Standard error shown in brackets.	Additions to the population/m^2 per annum	Percentage mortality
R.acetosella	3	120 (12)	0	100
R.acetosella	4	1725 (166)	0	100
R.crispus and R.obtusifolius	1 & 6	5400 (97)	0.4	99.9
R.crispus	2	6000 (1149)	17	99.7
R.obtusifolius	5	1800 (135)	5	99.7

Additions to the population/m^2 per annum =

$$\frac{\text{number of plants gained}}{\text{area of plot in square meters}}$$ (see tables 4,5,6, and 7.

The number of *R. acetosella* seedlings which survived to become mature plants must have been extremely low at these two plots. The few seedlings observed during the population dynamics survey did not survive.

(8) Leaf Turnover Rates

Maximum leaf turnover rates in *R. crispus* and *R. obtusifolius* were 0.8 of a leaf each day. Leaf turnover rates in *R. acetosella* plants at the planted plots with 200 or more leaves reached 8.1 leaves each day. This was much higher than the leaf turnover rates observed in the *R. acetosella* field plots.

III. ALLOCATION OF RESOURCES DATA

(1) The Allocation of Resources and Reproductive Effort in *R. crispus* and *R. obtusifolius*

(a) Introduction: A total of 150 plants of each species were sampled at five sampling times between July 1975 and January 1976. The actual dates were 13 July, 13 September, 14 November, 9 December and 24 January. None of the plants taken in the first sample had started to flower. The results of the last sample were discarded as most plants in the last sample had shed some of their seed and most of their leaves, so that estimates of the standing energy content of different organs were not proportional to their cost.

(b) Energy determinations and joules per gram of different organs: The energy determinations for each organ of each plant were made separately and converted to

percentages of the total energy content of each plant. There were no consistent differences in the joules per gram for each plant organ at different plots. However, the joules per gram varied between organs of the same species. In *R. crispus* the mean energy content was 21.6 j/g for seeds, 19.2 j/g for panicles, 18.3 j/g for leaves and 16.6 j/g for roots. In *R. obtusifolius* the mean energy contents for the same organs were 19.7 j/g, 18.5 j/g, 18.5 j/g and 17.0 j/g respectively. In both species, only seeds and roots were significantly different ,(Students t value = 2.7, $P<0.05$).

(c) The allocation of energy to roots and leaves: There were no consistent differences in the proportion of resources allocated to roots at different sampling times in either species. The decrease in the proportion of energy allocated to $\text{roots}_{\wedge}^{\text{plus stems}}$ in later samples was not biologically significant, because it represented a decrease in the proportion of total energy present in roots, but not a decrease in the absolute energy content. The decreasing proportion of energy present in $\text{roots}_{\wedge}^{\text{plus stems}}$ was caused by the development of panicles and seed. For both species, the difference in the mean proportion of energy present in the roots at the planted plots (8 and 9) and the other plots was significant ($P < 0.05$) (Figs 18 and 19).

The plots differed considerably in plant density (Table 16). As the density of *R. crispus* plants increased, a higher proportion of their resources was allocated to roots. A similar situation was present in *R. obtusifolius*. The mean percentage of energy allocated to $\text{roots}_{\wedge}^{\text{plus stems}}$ in all plots of both species was 62%.

Table 16. REPRODUCTIVE EFFORT IN *R. crispus* and *R. obtusifolius*

Species	Plot No.	Plant density/m^2	Mean reproductive effort of all plants which produced panicles or flowered				Mean reproductive effort of all plants at each plot	Proportion of plants which reproduced
			Sample 2	Sample 3	Sample 4	Mean reproductive effort		
R. crispus	8	1.0	-	35	46	39	31	0.85*
	1	1.7	41	52	43	42	27	0.60
	2	33.0	42	47	32	40	21	0.53
R. obtusifolius	9	1.0	6	19	28	19	15	0.71
	6	1.7	7	28	23	22	12	0.46
	5	11.1	11	15	24	20	7	0.34

Reproductive effort measured in per cent allocation.

*Does not include sample 2 in which no plants flowered.

The mean percentage of energy allocated to leaves in all plots was 22% for *R. crispus* and 29% for *R. obtusifolius*. The proportion of energy present in leaves (both panicle and basal leaves) decreased in later samples (Figs 18 and 19). In this case the change was biologically significant and reflected not only a relative decrease (due to the development of panicles and seed) but was also due to the shedding of many leaves and a lower rate of leaf development at the onset of reproduction. The mean proportion of energy allocated to leaves was higher in the planted plots (those with the lowest plant density) of each species.

The mean proportion of energy allocated to leaves plus roots for all plants over all samples decreased slightly in both species as density decreased (Figs 18 and 19).

(c) The allocation of resources to reproduction: sexual

The allocation of resources to reproduction (reproductive effort) was defined as the combined percentage allocation to panicles and seeds. If the reproductive effort at each plot (for all samples in which some reproduction took place) was considered, rather than per plant, reproductive effort increased as plant density decreased in both species (Table 16). However, this change in reproductive effort was not due to changes in the reproductive effort of individuals but to the increasing proportion of plants which reproduced as density decreased (Table 16).

The mean reproductive effort of all plants that reproduced at all plots was 40.5% (standard deviation

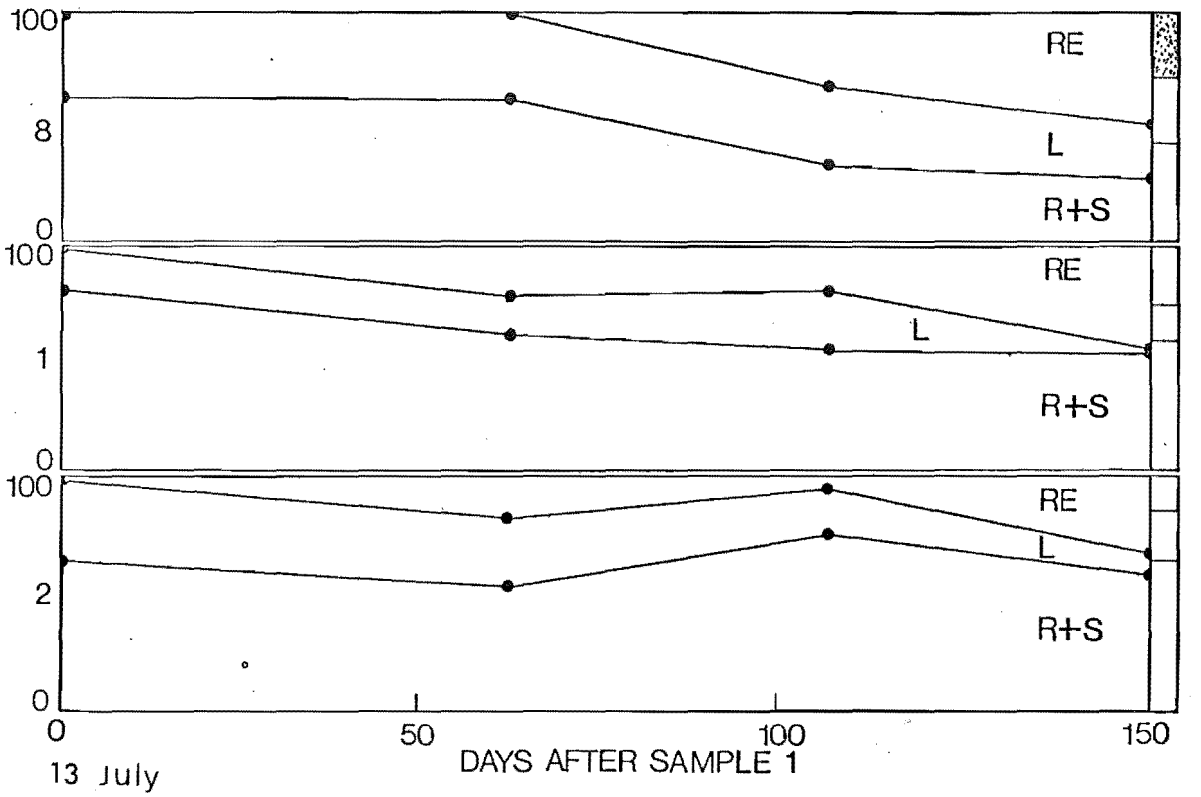


Fig. 18. The percentage of energy expended on reproduction, leaves and roots plus stems in *R. crispus* plants at successive sample times at three plots. Reproductive effort (RE), leaves (L), and roots plus stems (R + S). The bars on the right of the graph show the mean energy allocated to reproduction (stippled), leaves and roots plus stems for all samples.

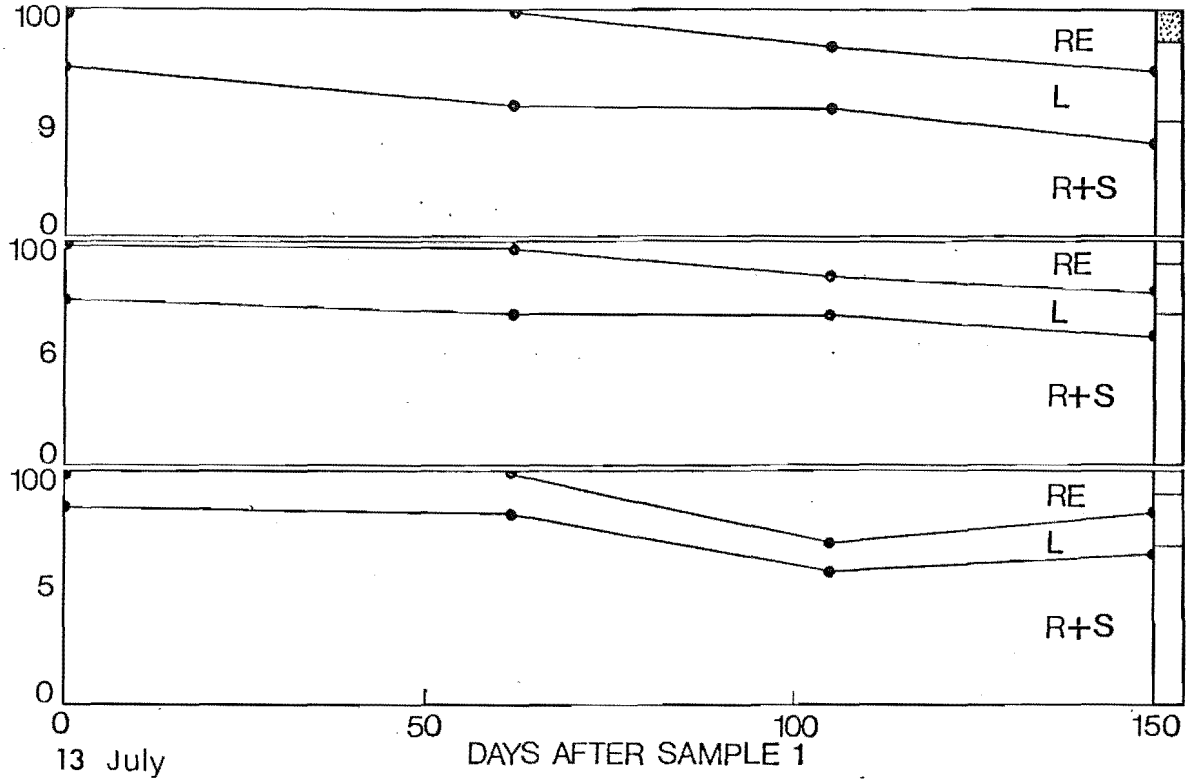


Fig. 19. The percentage of energy expended on reproduction, leaves and roots plus stems in *R.obtusifolius* plants at successive sample times at three plots. Reproductive effort (RE), leaves (L), and roots plus stems (R + S). The bars on the right of the graph show the mean energy allocated to reproduction (stippled), leaves and roots plus stems for all samples.

= 13.2) for *R. crispus* and 20% (standard deviation = 8.9) for *R. obtusifolius*. T-tests showed that this was significantly different ($t = 8.48$, $P<0.01$)

If the reproductive effort of the plants at each plot is determined only from plants which reproduced, the mean percentage of energy allocated to reproduction increased in later samples. This was because plants reached the point of maximum reproductive effort between the third and fourth samples. In plots 9 and 5, maximum reproductive effort occurred slightly later than in other plots. Thus later samples showed that the energy present in reproductive tissues had decreased as some seed and panicles were lost, and the rate of leaf production increased.

The mean reproductive effort of plants which reproduced did not vary between plots for each species (Table 16 and Fig. 20). (This was also shown by the very small difference between the ratio of reproductive effort per plot to the proportion of plants which reproduced per plot. For *R. crispus* the ratios were 43, 45 and 39 for plots 8, 1 and 2 respectively, and for *R. obtusifolius*, 21, 26 and 20 for plots 9, 6 and 5 respectively.)

(d) The relationship between reproductive effort and total plant energy: The relationship between total plant energy and reproductive effort was confounded by the varying numbers of leaves retained by different plants. Because the proportion of energy present in roots did not vary, total root energy is directly related to total plant energy and is not subject to short-term variation, it was used as a relative measure of total plant energy. Therefore the ratio of energy allocated to reproduction to total root

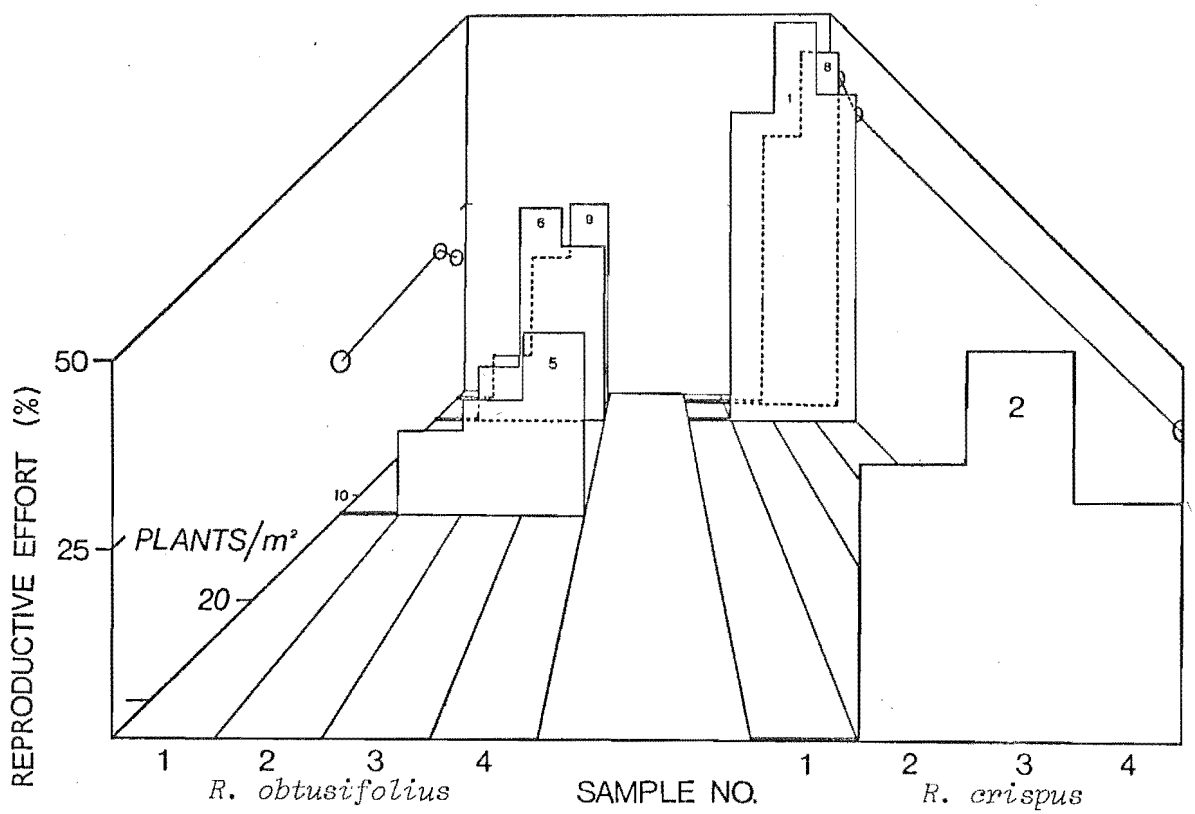


Fig. 20. Reproductive effort of *R. crispus* and *R. obtusifolius* plants at various densities. Reproductive effort was measured in terms of the joules allocated to reproductive panicles plus seed as a percentage of the total joules of the plant.

The mean reproductive effort per sample (excluding the first sample in which no reproduction took place) is plotted on the y-z planes on either side of the figure.

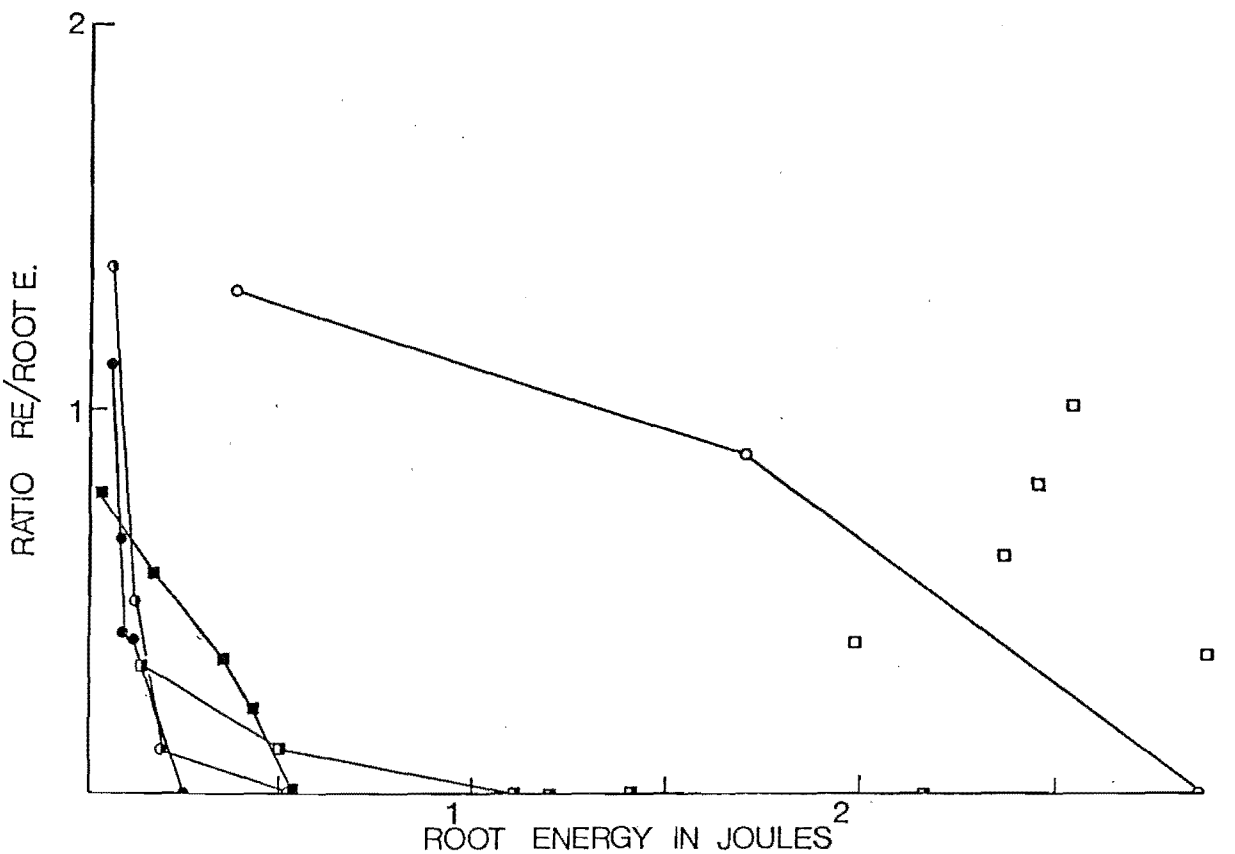


Fig. 21 The relationship between "mofified" reproductive effort and plant energy (estimated by root energy).

R. crispus plots 8 (○), 1 (◐), 2 (●).

R. obtusifolius plots 9 (□), 6 (◨), 5 (■).

See Appendix 3 for Spearman's rank correlation coefficients.

energy was plotted against total root energy to obtain the relationship between "modified" reproductive effort and plant "status". The relationship is shown in Figure 21 for the fourth sample of all plots. The curvilinear relationship between "modified" reproductive effort and total root energy for the plants in some plots but not others precluded regression analysis.

For both species (except *R. obtusifolius* at plot 9), plants with higher root energy tended to have a lower "modified" reproductive effort within plots. See Appendix 3 for significance levels.

(2) The Allocation of Resources in *R. acetosella* Plants Under Three Stress Treatments

(a) Data variability: For this study, eight harvests of three plants were sampled from each of the three stress treatments over a total period of 150 days. Altogether 72 plants were harvested. Five were discarded after analysis because they had not been watered properly and exhibited extreme deviations from the responses typical for their stress treatment. A little less than half of the plants produced neither vegetative offspring nor flowers, the remainder produced either vegetative offspring or flowers, or both. Thus the number of plants falling into each category was low and was further reduced by the division of plants by sex. The low number of plants in each category contributed to the variability between results and made statistical analysis difficult. Statistical analysis was further complicated by the different developmental stages of the plants being sampled, but despite these limitations the data indicate some general trends.

(b) The joules per gram of each organ under different stress treatments: There were no significant differences in the joules per gram for each plant organ under the three stress treatments. However, the joules per gram did vary between different organs. This showed that energy determinations were more representative of the net cost of an organ than dry weights. Seeds had a mean energy content of 20.9 joules per gram of dry weight compared to 18.4 and 17.9 for roots and leaves respectively.

(c) The relationship between the effective stress on plants and net production: The effective stress imposed by different pot sizes was gauged by the total biomass and energy content of all plants under each stress treatment and by the increment in total net energy per harvest.

The total biomass for all plants harvested within each stress treatment was 12.2 g, 61.7 g and 137.2 g for the high, medium and low stress treatments respectively (a ratio of 1: 5.1: 11.2 compared to a pot volume ratio of 1: 8: 18). The total energy contained in plant matter in joules for each stress treatment was 241.6, 1074.4 and 2198.1 (a ratio of 1: 4.4: 9.1). Thus the total net energy of plants in each stress treatment was roughly parallel to the pot volume.

The graph of total joules per harvest for each stress treatment (Fig. 22) shows a similar difference between treatments. The energy present at the first harvest and the subsequent increments in energy between harvests was greatest with the lowest stress and intermediate with medium stress. The average quantity of energy per unit time at

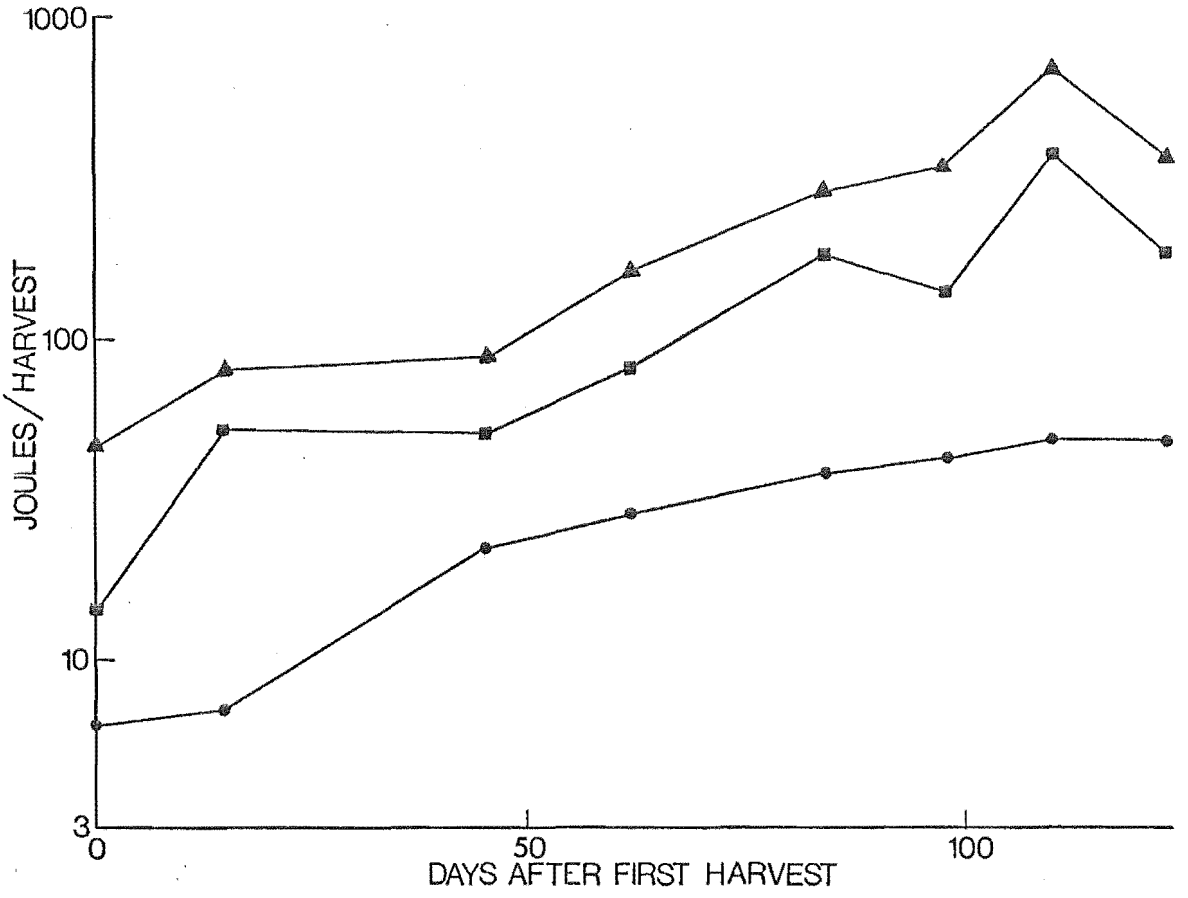


Fig. 22. Total joules per harvest for *R. acetosella* plants under three stress treatments. High stress (●), medium stress (■) and low stress (▲).

See Appendix 4 for raw data and regression equations.

which energy was accumulated did not differ markedly between stress treatments.

(d) Developmental precocity in each stress treatment: Plants which were subject to high and medium stress did not produce panicles until the fifth harvest, whilst plants in the low stress treatment had initiated panicle development by the first harvest. The production of vegetative offspring was delayed until the third harvest in all treatments.

The number of plants exhibiting vegetative and/or sexual reproduction of any type increased as stress decreased. Plants in the high stress treatment were more variable in habit and exhibited erratic developmental tendencies when compared to plants in the lower stress treatments. Although the plants in the high stress treatment had smaller leaves and panicles than those in the other two treatments, they did not show signs of abnormal development or physiological stress such as discoloured leaves. This indicated that their reduced size and slower development was a normal, plastic response within the adaptive norm of this species, rather than an inability to tolerate the conditions to which they were subjected.

(e) The allocation of energy to roots and leaves under the three stress conditions: The mean percentage of energy allocated to roots for plants that produced either vegetative offspring, flowers, or both almost doubled from the high to low stress treatments. The percentage allocation to leaves did not change so markedly (Table 17).

There were no consistent differences in the

Table 17. THE ALLOCATION OF ENERGY TO NON-REPRODUCTIVE ORGANS IN MALE AND FEMALE *R. acetosella* PLANTS

ORGAN	STRESS TREATMENT					
	HIGH		MEDIUM		LOW	
	Male	Female	Male	Female	Male	Female
ROOTS	47.5	21.4	41.8	44.5	61.8	70.3
	(39.6)		(47.3)		(63.4)	
LEAVES*	19.7	15.2	26.3	21.5	16.8	18.1
	(21.6)		(29.8)		(22.9)	

All results in percentage allocation.

* Panicle leaves excluded.

Brackets include the mean percentage allocation for males and females together.

See Appendix 5 for raw data and sample sizes.

Table 18. THE NUMBER OF VEGETATIVE OFFSPRING PRODUCED PER PERCENT ALLOCATED TO VEGETATIVE OFFSPRING PRODUCTION

	STRESS TREATMENT		
	High	Medium	Low
Number of plants producing offspring	10	10	15
Total number of vegetative offspring produced/treatment	23	68	317
Mean number of vegetative offspring/plant	2.3	6.8	21.1
Percentage allocation to vegetative offspring production	6.3	3.5	5.8
Allocation per individual vegetative offspring	0.27	0.05	0.02

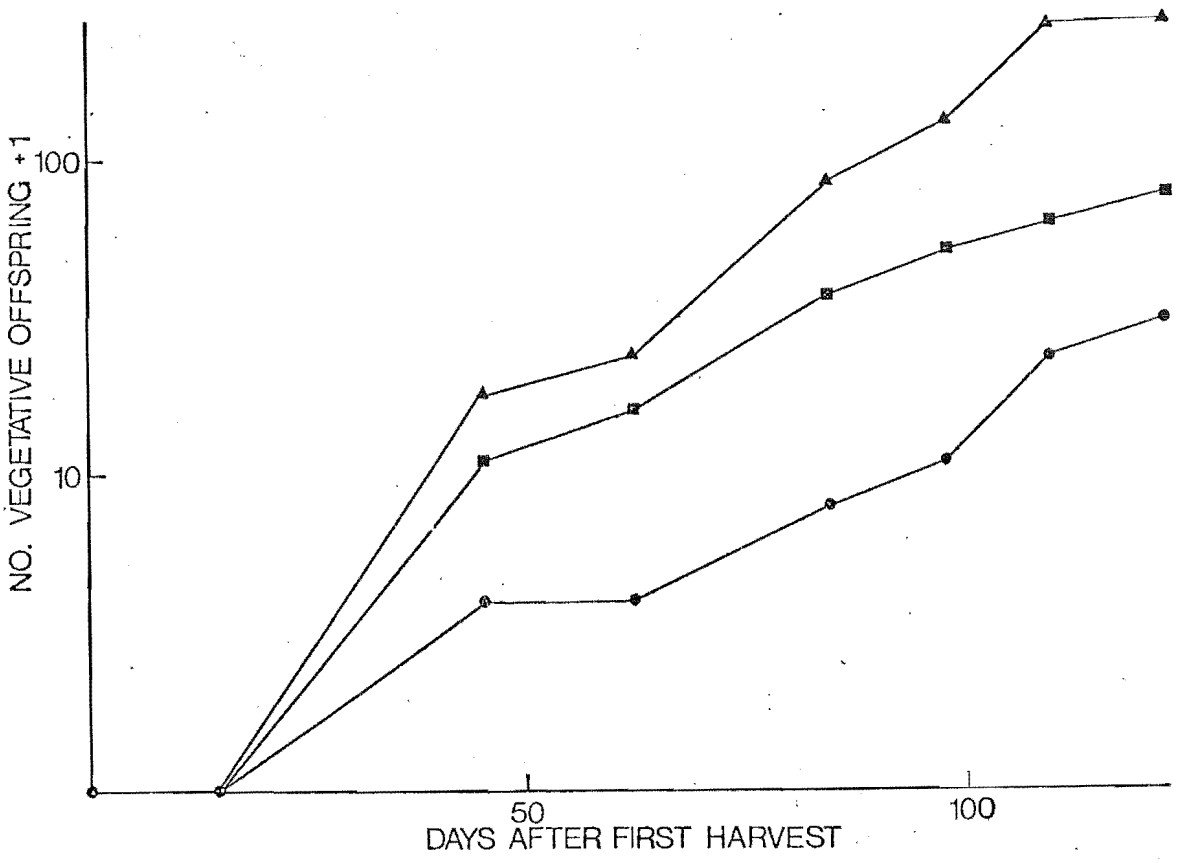


Fig. 23. Cumulative number of vegetative offspring +1 produced by R. acetosella plants plotted on a log scale for each harvest under three stress treatments. High stress (●), Medium (■) and Low stress (▲).

Regression equation:		$s_{b_{y.x}}$
High:	logY= -0.1366 + 0.0130X	0.00102
Medium:	logY= 0.1663 + 0.0168X	0.01559
Low:	logY= -0.0253 + 0.0218X	0.00169

Significance of differences between slopes:

H-M t = 0.24 NS
H-L t = 6.52 P<0.01
M-L t =19.84 P<0.01

proportion of energy allocated to either roots or leaves between male and female plants (Table 17).

(f) The allocation of resources to vegetative reproduction: Ten, 10 and 15 plants in the high, medium and low stress treatments respectively produced at least one offspring. The total number of vegetative offspring produced by all plants in each stress treatment increased as stress decreased at a much greater rate than the numbers of plants which produced vegetative offspring (Table 18).

The rate at which vegetative offspring were produced differed markedly between treatments (Fig. 23). After an initial stage, during which few vegetative offspring were produced, plants under all three stress treatments increased the rate of vegetative offspring production between harvests 4 and 5. The rate of offspring development increased greatly as stress decreased.

The percentage of net energy allocated by parents to vegetative offspring cannot be measured directly. This was determined experimentally using radioactive tracers and plants grown in conditions equivalent to the medium stress treatment. The total allocation of energy by parents to vegetative offspring decreased as offspring size increased, until for vegetative offspring weighing more than 0.05 g the allocation was insignificant (Fig. 25). Thus it is necessary to determine the energy content of each vegetative offspring independently and calculate the proportion of that energy received from the parent plant. Practical limitations on the minimum size of offspring which could be analysed prevented this from being done directly. To determine the total energy allocated by a parent to its offspring, the

relationship between total energy per vegetative offspring and total leaf length was calculated from Fig. 24: sum of leaf length = 80.5 times total joules of vegetative offspring. This enables the energy constant (and weight) of every vegetative offspring to be estimated and compared to the calibration curve obtained from the radioactive tracer study. This study related offspring energy content (and weight) to the proportion of energy it had received from its parent. The energy contained in vegetative offspring where the parental allocation became insignificant was 0.89 joules. Thus the energy allocated to offspring below this energy content could be estimated at a maximum limit of 0.89 joules for vegetative offspring with a net energy greater than this.

Using this method the percentage of energy allocated by parent plants without flowers to their vegetative offspring was obtained (Table 19). The number of vegetative offspring produced and the rate at which they were produced were inversely related to the stress level and therefore directly related to plant size. However, the percentage of energy allocated to vegetative reproduction by plants under different stress treatments (or different net energy) did not vary significantly. This, in combination with Figures 23 and 25, suggests that there is a minimum size which must be reached by parent plants before they will allocate energy to vegetative offspring. After this size is attained, plants allocate a constant proportion of their resources to the production of vegetative offspring.

As stress decreased, the number of vegetative offspring produced per unit of energy allocated to vegetative offspring production increased markedly (Table 18).

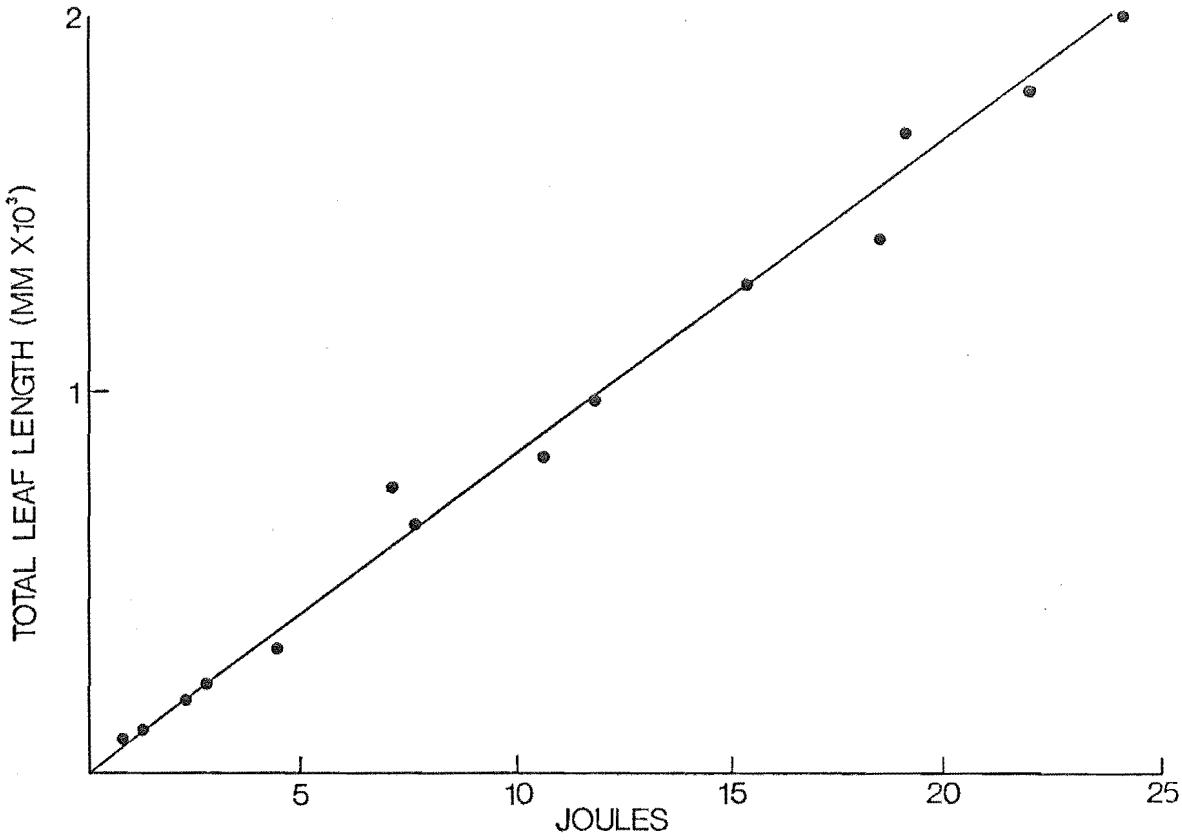


Fig. 24. Total leaf length of *R. acetosella* vegetative offspring related to vegetative offspring energy.
See Appendix 6 for raw data.

Regression equation= Leaf length=26 plus 80.5 energy in joules.

Table 19. THE ALLOCATION OF ENERGY TO VEGETATIVE OFFSPRING

	STRESS TREATMENT		
	High	Medium	Low
Parents without flowers	9.0	3.0	8.3
Parents with flowers	3.6	3.9	3.6

All results in percentage allocation.

See Appendix 7 and 8 for raw data

Table 20. THE ALLOCATION OF ENERGY TO SEXUAL REPRODUCTION FOR MALE AND FEMALE PLANTS UNDER THREE STRESS TREATMENTS

BY MALE AND FEMALE PLANTS	STRESS TREATMENT		
Seed or flower without panicles	High	Medium	Low
Female plants	18.6	5.4	0.8
Male plants	0.8	1.6	1.0
Ratio of male to female per cent allocation *	0.05	0.29	1.25

See Appendix 5 for raw data.

All results in percentage allocation except *.

(g) The allocation of resources to sexual reproduction: With the exception of two plants, plants that flowered also produced vegetative offspring. This made it impossible to compare the allocation of resources to sexual reproduction in plants with and without vegetative offspring.

Within the 150 days over which the experiment was run only two plants in the high stress treatment flowered, the first of these in the fifth harvest. The production of flowers was also delayed until just before the fifth harvest in the medium treatment. By the eighth harvest eight plants had flowered. In the low stress treatment, one plant had produced a reproductive panicle by the first harvest, and six by the fourth harvest. By the eighth harvest a further six plants had reached various stages of flowering.

The total number of flowers or seeds produced by all plants in each treatment was approximately 600, 3300 and 6300 for the high, medium and low stress treatments respectively. The mean number of seeds produced by each plant in each treatment was 300, 413 and 1050 for the high, medium and low treatments respectively.

The mean percentage of energy allocated to sexual reproduction was 8.2% in females and 1.1% in males.

The results indicate that the percentage of energy allocated to flowers and seeds in females decreases markedly as stress decreases. In males there was no trend in the allocation of energy to flowers. Hence the relative amount allocated by males compared to females increases as stress decreases (Table 20).

The amount of energy allocated to reproductive panicles in males and females showed no consistent differences. The total percentage of energy allocated in males and females to seed plus flowers or reproductive panicles decreased as stress decreased (Table 20).

It was not possible to accurately calculate the number of male flowers and seed which could be produced per joule from the figures available in this experiment, because the stage of seed maturity and flower development was not the same for all plants.

(h) The allocation of energy to vegetative offspring in plants which produced seed and vegetative offspring: The percentage of energy allocated to vegetative reproduction in plants which also flowered was similar for the three stress treatments (Table 19). This was decreased if the plants flowered. The percentage of energy which was allocated to sexual reproduction decreased markedly in females as stress decreased (Table 20).

(3) The Movement of Metabolites Between the Parent and Offspring in *R. acetosella*

(a) Establishing the optimum sampling time: The amount of ^{14}C translocated was measured by the ratio of disintegrations per minute (DPM) per gram of offspring

tissue to the DPM per gram of parent tissue. After one hour a ratio of 0.11 was reached. After two days the ratio had increased to 0.48, and reached a peak between four and six days at ratios of 0.49 and 0.47 respectively. A ratio of 0.46 after ten days indicated that further translocation was not taking place.

Thus the shortest sampling interval that allowed almost maximal translocation was approximately five days. The distance between the parent and offspring was not correlated with the amount of material translocated over this period.

(b) The amount of material translocated between the parents and their offspring: The high variability inherent in this method of radioactive tracer analysis has two principal sources. The absorption of radioactive CO_2 by plants is not directly related to their size and is further complicated by the accessibility of the gas to the leaf and the residuum of gas which cannot be evacuated from the plastic bag before the radioactive CO_2 is introduced. Experimental error is necessarily high when high DPM's are recorded and dry weights are extremely low.

The proportion of a parent's resources allocated to its offspring was calculated by dividing the ratio of DPM of the offspring to the total DPM (of both parent and offspring) by the weight of the offspring. This figure represents the proportion of each gram of parental dry weight donated to each gram of offspring. Similar figures were calculated for the amount of material translocated from the offspring to the parent. Both of these sets of figures were

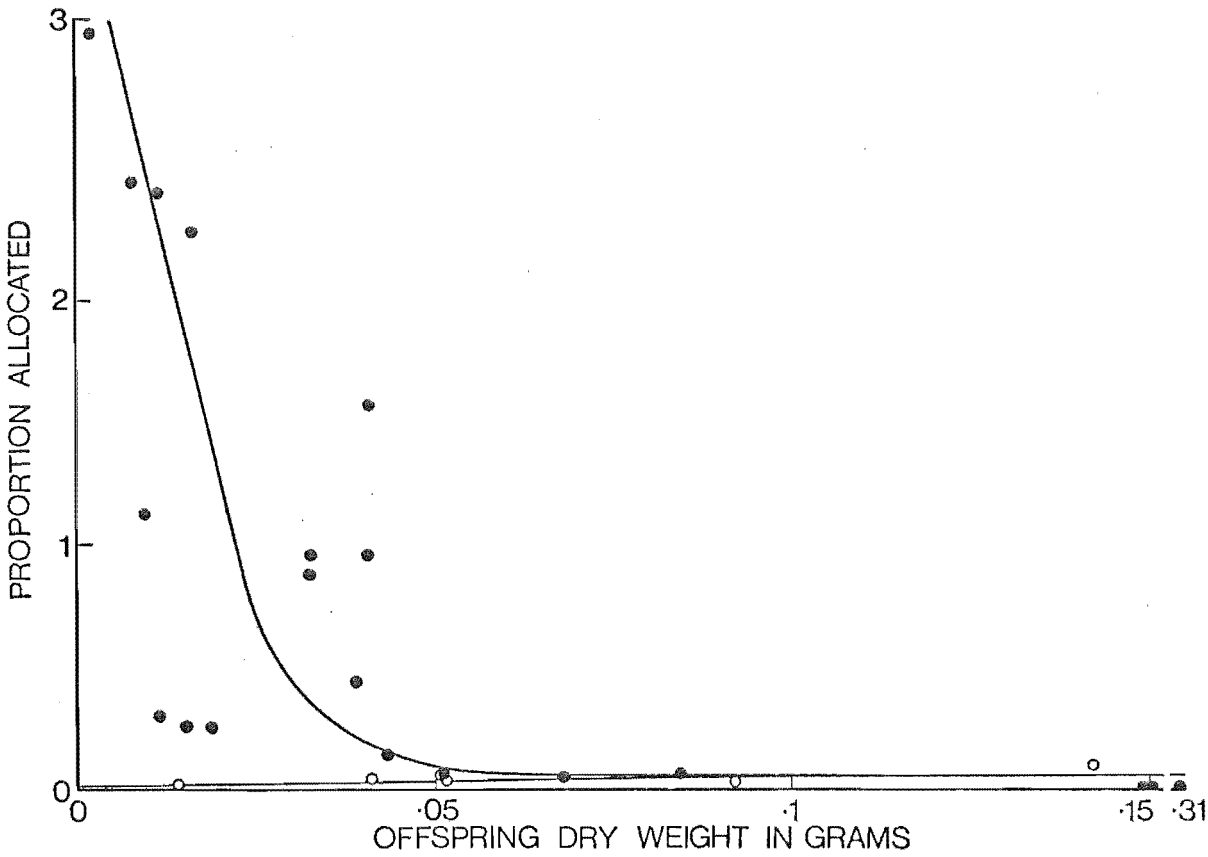


Fig. 25. Proportion of parental resources allocated to offspring of varying sizes and the proportion of vegetative offspring resources allocated to parents in *R. acetosella*. The proportion allocated was obtained by dividing the recipient DPM by the donor plus recipient DPM. Allocation by parents to offspring and offspring to parents shown by (●) and (o) respectively.

See Appendix 9 and 10 for raw data and regression equations.

plotted against offspring weight in Figure 25.

The mean proportion of the material assimilated by a parent that was allocated to each offspring was 2.44%. The mean proportion of material assimilated by offspring and allocated to their parents was 0.47%. This difference was far greater for offspring weighing less than 0.05 g, when the proportion allocated by parents to their offspring was 3.84% compared to 0.02% for the amount allocated by offspring to their parents.

The graph indicates that the allocation to offspring from their parents decreased rapidly as offspring weight approached 0.05 g. For offspring weighing more than 0.05 g, the proportion of the parent's resources allocated to an offspring was approximately equal to the proportion of the offspring's resources allocated to the parent. Although the proportion of material allocated by parents to offspring and offspring to parents was similar for offspring weighing more than 0.05 g, the absolute contribution of offspring to parents was far lower than that of parents to offspring. (This was because the mean offspring weight was 0.086 of the mean parental weight.) Thus, although the percentage allocation by parents to offspring weighing less than 0.05 g was 192 times greater than the allocation of offspring to parents, the absolute allocation was 2000 times greater.

For offspring weighing more than 0.05 g, the absolute allocation of parents to offspring only exceeded that of offspring to parents by a factor of three, since mean weights of parent and offspring were 0.42 g and 0.14 g respectively.

(c) Analysis of single plants in detail: The

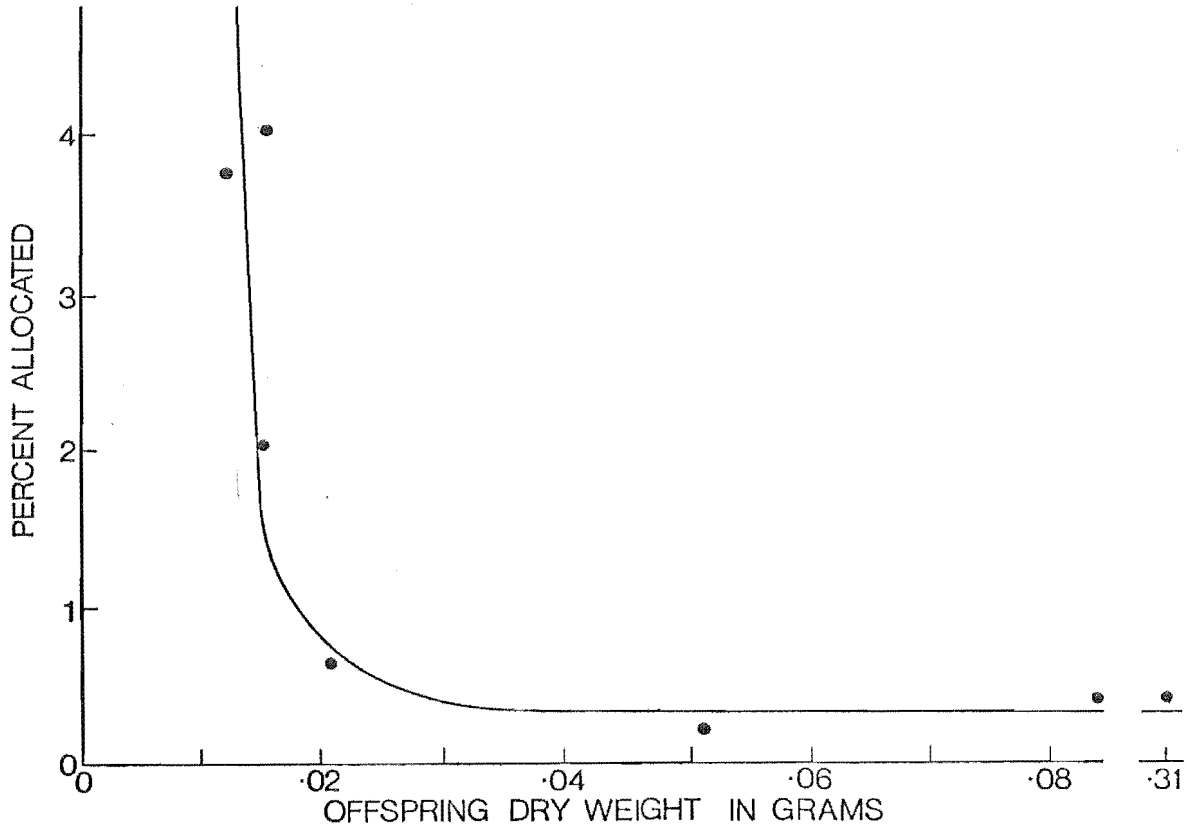


Fig. 26. Allocation of resources by a single *R. acetosella* parent to vegetative offspring of various sizes. The percentage of resources allocated was calculated by dividing the recipient vegetative offspring DPM by the total DPM for the parent and all offspring. curve fitted by eye

See Appendix 11 for raw data and regression equation.

detailed analysis of single plants and all their offspring permitted percentage allocations to be calculated directly. This type of analysis is more accurate than the type described above because the total DPMs for the parent plant and all offspring are known. However, the results were necessarily restricted to small samples.

The analysis of plants in this way showed similar trends to the method of analysis described above. The percentage of the total DPMs in each of seven offspring from one parent is graphed against offspring weight in Figure 26. As offspring weight decreased so did the parental allocation to the offspring. With increases in offspring weight above 0.04 g, the parental allocation to the offspring did not decrease further.

IV. SEED GERMINATION RESULTS

(1) Maximum Germination Percentages for *R. crispus* and *R. obtusifolius* Under Ideal Conditions

The mean percentage germination of five samples of *R. crispus* seeds germinated under ideal conditions was 88%, with a standard deviation of 1.9%. *R. obtusifolius* gave 98% germination and a lower standard deviation of 1.4%.

(2) Comparison of Weights and Germination Percentages of Seed from Primary and Secondary Branches of the Panicle

The mean weights of the seeds and perianth segments of the *R. crispus* plants on both the main and secondary branches were significantly greater ($P < 0.05$) than those of

Table 21. WEIGHTS OF SEEDS PLUS PERIANTHS FROM THE MAIN AND SECONDARY BRANCHES

Weight of 100 Seeds borne on:	*R. crispus*		*R. obtusifolius*	
	Main branches	Secondary branches	Main branches	Secondary branches
Mean weight in grams	0.1424	0.1412	0.1118	0.1125
S^2	0.000008	0.000049	0.000066	0.000047

There were significant differences ($P < 0.05$) between the weight of *R. crispus* seeds borne on the primary branches and both classes of *R. obtusifolius* seeds, and *R. crispus* seeds borne on the secondary branches and both classes of *R. obtusifolius* seeds.

Table 22. WEIGHTS OF SEEDS BORNE ON THE MAIN AND SECONDARY BRANCHES

Weight of 100 Seeds borne on:	*R. crispus*		*R. obtusifolius*	
	Main branches	Secondary branches	Main branches	Secondary branches
Mean weight in grams	0.0702	0.0699	0.0698	0.0693
S^2	0.000004	0.000004	0.000007	0.000020

There were no significant differences between any of the classes.

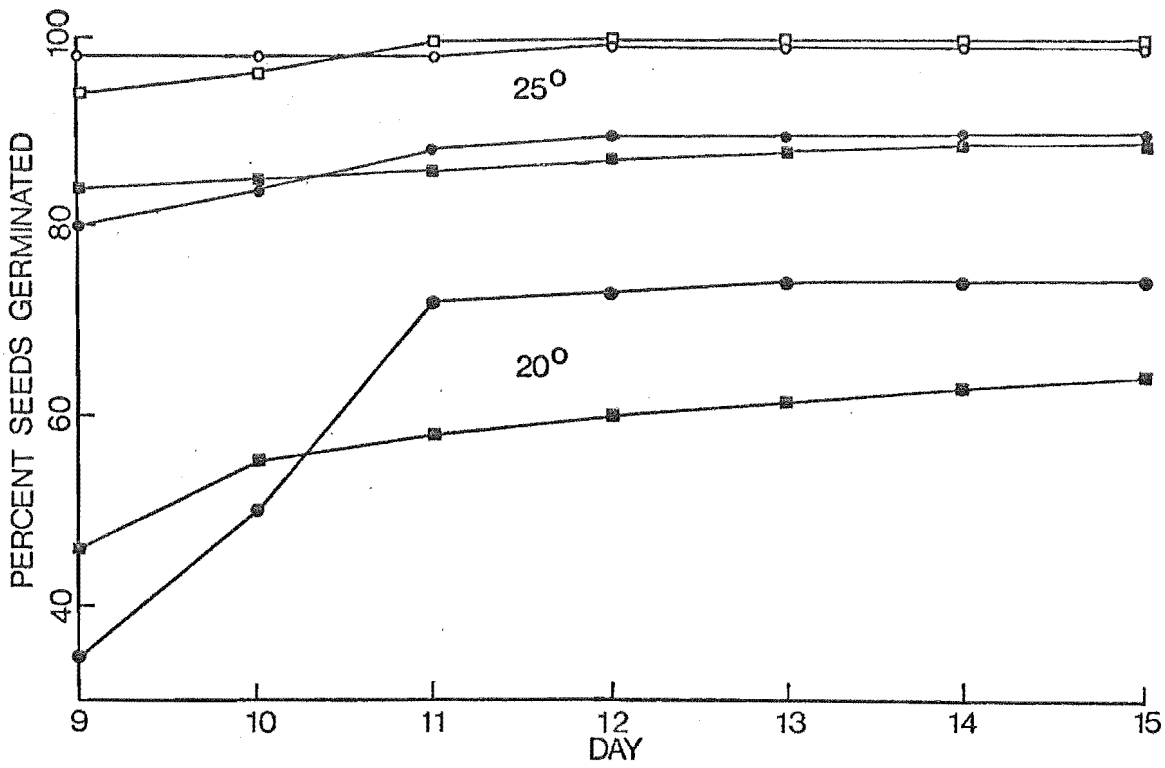


Fig. 27. Germination of *R. crispus* and *R. obtusifolius* seeds borne on the primary and secondary branches of the panicle. *R. crispus* seeds borne on primary (■) and secondary (●) branches. *R. obtusifolius* seeds borne on primary (□) and secondary (o) branches.

Results of R. obtusifolius germinated at 20
have been omitted for clarity.

R. obtusifolius on both the main and secondary branches. There was no significant difference in the weights of the seeds plus perianths within each species (Table 21).

After removal of the perianth segments, the mean weights of the seeds done were not significantly different between or within species (Table 22). Thus the difference between the two species of the seeds plus perianths was due to the greater development in *R. crispus* of perianth segments, forming larger valves and tubercles. The very low standard deviations indicate that there was very little difference in mean weight between plants for seeds in the same class.

Neither experiment showed a significant difference in final germination percentage ($P < 0.05$) between *R. obtusifolius* seeds borne on primary or secondary branches, either within or between experiments. *R. crispus* seeds behaved differently. At the higher temperature, they exhibited significantly lower overall germination percentages ($P < 0.05$) than *R. obtusifolius* seeds (Fig. 27). The small difference between the germination percentage of seeds from the main and secondary branches was not significant ($P < 0.05$). Lower temperatures reduced germination percentages. However, at the lower temperature, seeds from the primary branch had a significantly lower ($P < 0.05$) germination percentage than those from secondary branches. Thus, different germination temperatures affected seeds borne on primary and secondary branches differently.

The percentage of abnormal seeds borne on primary and secondary branches was not significantly different within either species. The percentage of normal seeds in each class are shown in Table 23.

Table 23. PROPORTION OF NORMAL SEEDS BORNE ON THE PRIMARY AND SECONDARY BRANCHES OF *R. crispus* AND *R. obtusifolius* PLANTS

	R. crispus		*R. obtusifolius*	
	Primary	Secondary	Primary	Secondary
Mean percentage of normal seeds	96.4	95.6	90.6	96.0
Standard deviation	2.18	2.18	2.60	2.35

There is no significant difference ($P < 0.05$) between samples except between *R. obtusifolius* seeds borne on primary panicles and both types of *R. crispus* seed.

V. SEED DISPERSAL RESULTS

(1) Dispersal of Seeds by Wind

The mean distances travelled by the seeds plus perianth segments of the three species were very similar, as was the mean distance travelled by seeds of *R. crispus* and *R. obtusifolius* without perianth segments. However, the maximum distance travelled by the seeds plus perianth segments of each species is different: 95 centimetres for *R. acetosella*, 65 centimetres for *R. crispus* and 75 centimetres for *R. obtusifolius* (Fig. 28). The *R. acetosella* seeds which travelled furthermost were visibly smaller than the majority of seeds.

Under field conditions where wind speeds are frequently many times higher than those used in this experiment, it is presumable that the differences between the distances travelled by the seeds plus perianth segments would be significant in terms of the relative distances over which the species were distributed.

(2) Dispersal of Seeds by Water

A difference in the ability of the seeds of the three species to remain floating was apparent as soon as they were put into water. After ten minutes of agitation, only 26% of *R. acetosella* seeds remained floating. After 20 hours, 17% of the seeds were still floating (Fig. 29). The number of seeds which remained floating over the next 120 hours decreased until after 140 hours when only 7% of the seeds remained floating.

All *R. crispus* seeds remained floating for the first 20 hours. After this time a steadily increasing number of

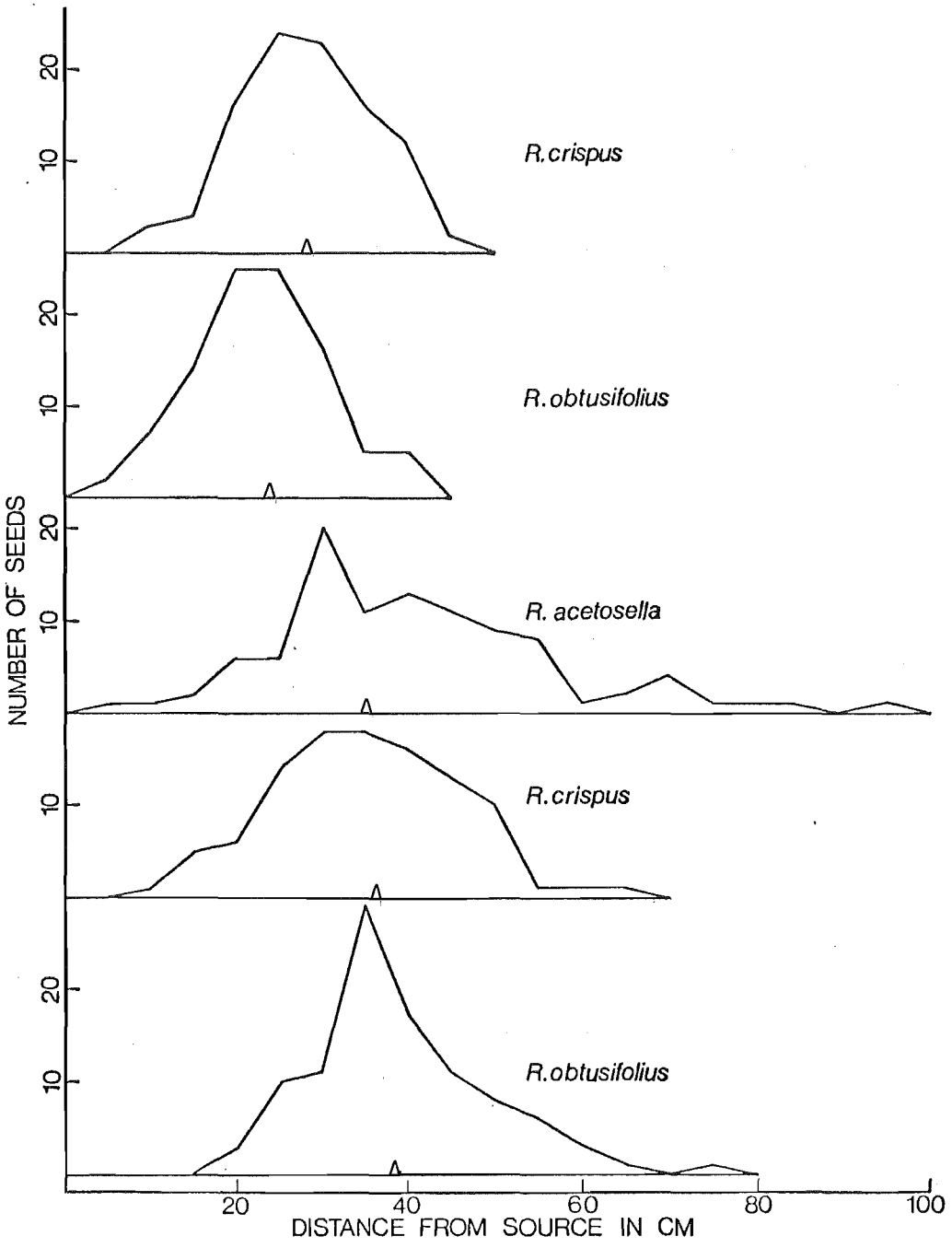


Fig. 28. The distances travelled by *Rumex* seeds in a wind tunnel. The two upper curves are for seeds without perianth segments. The three lower curves are for seeds plus perianth segments. Δ = mean

See Appendix 12 for raw data

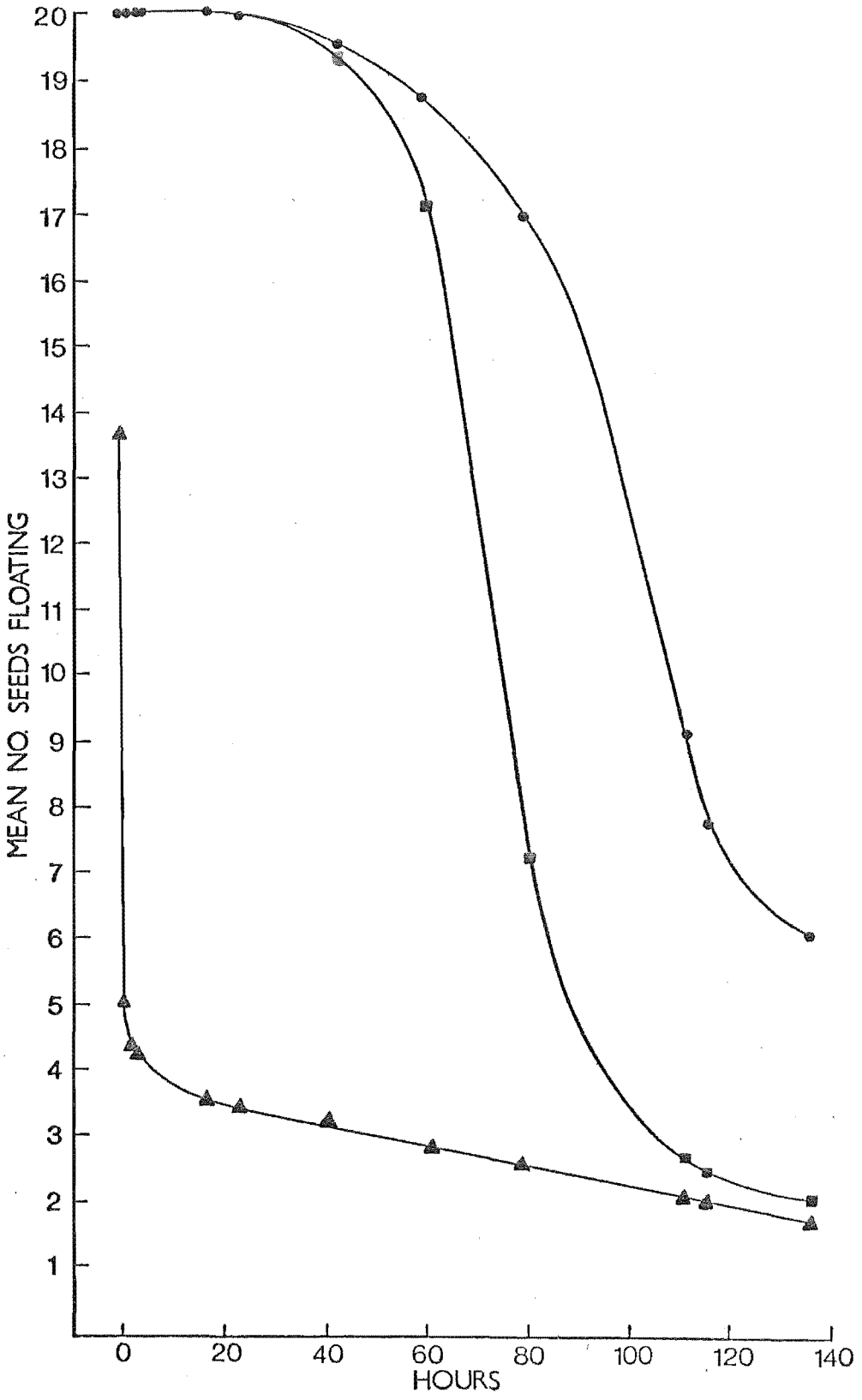


Fig. 29. The time *Rumex* seeds remain floating in agitated water. *R. acetosella* (▲), *R. crispus* (●) and *R. obtusifolius* (■).

See Appendix 13 for raw data.

seeds sank, although 30% of the seeds were still floating after 140 hours.

R. obtusifolius seeds exhibited similar characteristics to those of *R. crispus*. All seeds remained floating for the first 20 hours, after which there was a sharp decline in the number of seeds which remained floating. After 140 hours, 10% of the seeds were still floating. Until 60 hours there was no significant difference in the number of *R. crispus* and *R. obtusifolius* seeds which remained floating ($t = 3.95$, $P < 0.01$).

The percentage of *R. crispus* seeds which were still floating after 80 hours or more was significantly greater ($P < 0.01$) than the percentages of the seeds of the other two species ($t = 11.0$, $P < 0.01$).

(3) The Germination Percentages of Submerged Seed

After fourteen days, almost all seeds of all three species had sunk. The few seeds which remained floating had not germinated. Eighty per cent (SD = 7%) of the *R. obtusifolius* seeds had germinated whilst submerged compared to 26% *R. acetosella* (SD = 13%) and 7% (SD = 6%) *R. crispus*. The three samples were significantly different from each other. See Appendix 14 for test details.

(4) Seed Fall and Abscission Zone Structure

The external morphology and internal changes of the abscission zone between seed maturity and seed abscission for both species are discussed in Chapter VI.

The causes of these differences in abscission zone strength were related to morphological changes in the abscission zone by microscope studies. For some months

after seed maturity, the abscission layer in *R. crispus* consisted of an intact layer six to eight cells wide (Plate 14). Four months after seed maturity many of the cells had broken down (Plate 15). After a further two months almost all of the cells in the abscission zone had broken down, leaving intact only the cells which had been concerned with transport through the pedicel (Plate 16).

A similar series of changes took place in the abscission zone of *R. obtusifolius* plants. Plate 17 shows that the abscission zone consisted of about three layers of intact cells up to two months after seed maturity. Plate 18 shows an intermediate stage in which some of the cells have broken down.

It was not possible to determine the precise rate at which the abscission zone broke down, or the time at which the breakdown had started, because only four sets of samples were taken for each species.

VI. AGRICULTURAL EXPERIMENTS

(1) The Viability of *R. crispus* and *R. obtusifolius* Seeds at Various Stages of Maturity

The percentages of seeds germinating on panicles cut at a variety of seed developmental stages are shown in Table 24.

A small proportion of *R. obtusifolius* seeds were able to germinate when the panicles were cut at the beginning of the green seed stage. At this stage, *R. crispus* seeds did not germinate. The seeds of panicles cut when the majority of seeds were brown gave 77% germination for both species.

Table 24. PERCENTAGE GERMINATION OF SEEDS ON PANICLES CUT AT DIFFERENT STAGES OF SEED MATURITY

Developmental stage	Means *R. crispus*	*R. obtusifolius*
Flowering	0	0
Green seed	0	18 (0 - 48)
Mature, brown seed	77.2 (60 - 92)	77.2 (74 - 92)

The mean percentage of seeds which had germinated after 27 days (when germination ceased) are shown. Brackets indicate the range of germination percentages for seeds of different plants.

See Appendix 15 for raw data.

The large range of germination percentages for individual panicles within each category may be due to the expected differences between plants, and small differences in location or condition. Under the conditions of severe strain experienced by the excised panicles, very slight differences in the stage of maturity at which panicles are cut or the storage conditions may be critical in determining whether the seeds are capable of germination.

(2) The Ability of *R. crispus* and *R. obtusifolius* Plants to Regenerate from "Root" Fragments

The top part of the rootstock (which included parts of the crown) of *R. crispus* and *R. obtusifolius* plants underwent rapid regeneration in both the early and late spring trials. Within three weeks, both species were able to produce large numbers of healthy leaves and initiate the development of new root systems. The new shoots were developed from dormant buds on portions of stem. No portion consisting entirely of root in either the late or early spring trials regenerated. After three weeks these sections of root were starting to decompose.

CHAPTER V

DISCUSSION OF SURVIVAL RATES AND LIFE HISTORIES

I. INTRODUCTION

Sarukhán and Harper (1973) have recently stated that plants may exhibit survivorship curves that approximate the three main types* described by Deevey (1947), but that the only examples of mature plants with survivorship curves differing from Type II are those obtained from grasses. They attribute these departures to the fact that grasses are composed of many tillers, and the tiller, not the genotype (or whole plant), may be the appropriate unit to consider in survivorship studies. Here deviations from Deevey's (1947) Type II curve will be considered and related to fundamental differences in perennial plant life histories.

Long-term observations of individuals have seldom been carried out. The majority of these studies have described Type II survivorship curves. Harper (1967) has calculated survivorship curves from Tamm's (1956) data for three perennial herbs (*Sanicula europaea, Filipindula vulgaris* and

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*Type I curves are from populations with low mortality rates for most of the lifespan followed by high losses in older individuals.

Type II (diagonal) survivorship curves imply a constant mortality rate independent of age. Type II curves are also described as exponential decay curves.

Type III curves indicate high mortality rates early in life, followed by a period of low, nearly constant mortality.

Centaurea jacea), and shown that population numbers decreased exponentially. Sarukhân and Harper (1973) have similarly calculated survivorship curves which were all of Type II from data of Rabotnov (1958) for *Ranunculus acris* and *R. auricomus*, and Sagar (1959) for *Plantago lanceolata*. Type II curves were also obtained by Antonovics (1972) for *Anthoxanthum odoratum*, and Sarukhán and Harper (1973) for *Ranunculus repens*, *R. bulbosus* and *R. acris*.

A Type II curve implies that the degree of genetic adaptation to the environment remains constant with increasing size. Steady decay in population numbers also reflects a consistently favourable or unfavourable environmental regime (Williams 1970). If these conditions are satisfied, the probability of survival for plants at various life cycle stages are equal. This state implies that a member of a plant population which conforms to the exponential decay model might, in theory, persist indefinitely.

Two departures from the Type II curves will be considered. First, a lower probability of survival is sometimes associated with the younger life stages. Second, a lower probability of survival may be present in the later life stages of plants with cumulative growth. It will be shown that in plants growing from seed, a lower probability of survival in early life stages is a common phenomenon and results in a Type III survivorship curve.

II. SUCCESSIVE STAGES IN SURVIVORSHIP CURVES

(1) Survival in Early Life Stages

The varying survival rates of each life stage can be understood if the varying probabilities of survival of individual plants are considered. The causes of mortality in the whole population parallel those of individual members.

Harper (1967) has alluded to the discrepancy between Type III survival curves and Darwin's observations on the prevalence of severe early mortality. In most of the studies referred to above, younger life stages have been excluded from the survivorship curves. If seedling stages were included, overall survivorship curves would probably approximate Type III curves (Antonovic's 1972). Harper and White (1974) have also pointed out that as seedlings may emerge and die only hours later, population censuses underestimate recruitment and seedling mortality, and therefore bias Type III survivorship curves towards Type II. This was shown to be the case for *Ranunculus* species which exhibited a concave survivorship curve for the first 20-30 weeks before the population acquired a linear survivorship curve and constant half life (Sarukhán and Harper 1973). Similarly, in the most elegant life table analysis to date, Sharitz and McCormick (1973) found that the two annuals *Minuartia uniflora* and *Sedum smallii* produced Type III survivorship curves when seedlings were included.

The initial low probability of survival in the early life stages of plants can be attributed to a number of causes. The principal environmental causes of high mortality are: the unsuitability of the microsite in which many

seedlings are germinated, the high densities of other seedlings competing for similar resources (resulting in high levels of density-dependent mortality) and environmental unpredictability. Seedlings are vulnerable to periods without water or sunlight because they have not accumulated the reserves to carry themselves over short periods of adversity. The causes of high mortality intrinsic to the genotypes and phenotypes of the plants concerned include the presence of a large number of ill-adapted genotypes, juveniles having to live in a niche to which the adults are not adapted, and factors of scale. Some of the processes occurring within plants (e.g. transpiration, light reception, predator defense, etc.) may not operate as efficiently at the reduced scale of seedlings as they do in adults. For example, similar amounts of damage by a predator to a seedling and an adult may have disproportionately large effects on seedlings.

As seedlings in unsuitable microsites and with ill-adapted genotypes are selectively removed, and the remaining plants achieve a larger size, the probability of survival for the remaining plants increases.

(2) The Linear Portion of the Survivorship Curve

Once the early life stages have been passed, the probability of survival appears to be constant per unit time and results in linear survivorship curves. However, within the linear portion of survivorship curves, small and sometimes periodic fluctuations occur. These may be due to seasonal changes in mortality rates or to other causes.

The constant risk associated with the plateau phase

of the survival rate curve indicates that periodic variations in environmental stress are of secondary importance in this phase (Harper and White 1974). Although seasonal variation may cause minor changes to the probability of survival during this phase, changes occurring to the individuals (for example, increasing size) do not affect their long-term and continued adaptation to the environment.

(3) Survival in the Latter Life Stages

The presence of a decrease in the probability of survival in the latter life stages of some plants but not in others is indicative of a fundamental difference among perennial plants.

This change in the probability of survival which is evident in the latter parts of the survivorship curves of some species is probably related to physical limitations on increasing size, cumulative growth and the senescence of parts which cannot remain in continued use indefinitely. The gradual accumulation of damage from a variety of causes and the cost of reproduction may also contribute to the decrease in the probability of survival.

It is possible that some of the species with Type II survivorship curves would have ultimately exhibited a decreasing rate of survival if the studies had been carried out for longer periods.

The departures from constant probability of survival implicit in the first and last phases of the survivorship curve indicate that mortality occurs differentially at different life stages, and that the adaptation of each life

stage to the environment is different. That random environmental changes are not responsible for departures from a constant probability of survival is excluded since the survivorship pattern is repeated.

III. COMPOSITE SURVIVORSHIP CURVES

If a reduced probability of survival is present in both the early and late life stages, three phases can be distinguished in the survivorship curve (an initial concave portion followed by linear and convex portions). These merge into each other and together assume a concavo-convex form (Fig. 30A). The survival rate curve corresponding to such a survivorship curve approximates a hump (Fig. 30B).

Data corresponding to hump shaped survival rate curves have been reported for a variety of species, including human populations, Dall sheep (Murie 1944), female Himalayan thar (from Caughley 1966), hemlock-hardwood (using stem diameter as a measure of age, Goff and West 1975), a variety of range grasses (Canfield 1957), a variety of rice strains (Oka 1976) and the three *Rumex* species studied here.

IV. THE ADAPTIVE SIGNIFICANCE OF LIFE HISTORIES

(1) Introduction

Life histories evolve in response to the relationship between environmental predictability and the relative mortality rates of the various life stages of the organism (Stearns 1976).

For example, Charnov and Schaffer (1973) have shown

that despite the higher levels of seed set required in annuals compared to perennials (with similar probabilities of survival to reproduction), the annual habit is favoured in unpredictable environments with a low probability of adult survival. However, in situations where adult mortality is not high, a perennial population would increase at a greater rate than an annual population, the difference being proportional to the probability of an adult plant surviving from one year to the next.

Different life history strategies will alter the frequency at which individuals have to pass through each phase and the relative lengths of each phase.

Various life history strategies may circumvent, shorten, or lengthen particular phases.

(2) Vegetative Reproduction

One effect of vegetative reproduction is to circumvent the low probability of survival associated with the seed and seedling life stages. Plants which reproduce vegetatively are not prone to the same environmental and genetic causes of high mortality which affect seedlings. Vegetatively reproduced plants are not as dependent on microsite suitability or environmental constancy as seedlings because they have access to the reserve resources of the parent and become independent at a larger size than seedlings. These resources enable them to survive unsuitable microsites, short periods of environmental adversity and the disadvantages of scale to which seedlings are subject. Furthermore, if the environment is constant, the genetic load of ill-adapted genotypes is avoided because

the vegetative offspring are genetically identical to their parents, which have already been selected for their genetic suitability. Williams (1975) proposed that reduced genetic variability is one of the principal advantages of vegetative reproduction. A similar argument has been advanced by Harper and White (1974) who suggested that the high mortality of seedling stages associated with ill-adapted genotypes should be absent from apomicts. There is no information about the survivorship curves of such species.

The probability of survival of vegetatively produced "units" may be greater, equal to, or less than those of the parent.

(3) Life Histories and Survivorship Curves of *Rumex* Species

The *R. acetosella* populations studied here reproduced almost exclusively by vegetative means. Type I survivorship curves were expected for vegetatively produced populations in contrast to the concavo-convex curves which would have been obtained if seed reproduction had taken place. (This was shown by seedling mortality estimates.) As well as avoiding the low probability of survival associated with seed reproduction, vegetative reproduction may serve to maintain the genotype.

If the *R. acetosella* genotype or whole plant is considered instead of individual vegetative offspring, it is clear that the production of adventitious root buds prolongs the effective pleateau phase of the genotype.

In contrast to *R. acetosella*, the *R. crispus* and *R. obtusifolius* populations remained in the plateau phase

of their respective survivorship curves for extended periods. The effects of factors of scale and senescence were delayed by two mechanisms. In the above ground parts, the high turnover of shoots effected a periodic "rejuvenation" of the above ground parts. In the roots a different situation prevailed. As the roots became subject to the factors of scale and senescence, portions were replaced by new growth at the periphery of the plant. This was not common in the plants studied here, except in plot 6. At sites which have not been disturbed for some time this phenomenon is more frequent, and results in large, spread out plants colloquially referred to as "old man docks".

The extended period with constant probability of survival in both the *R. crispus* and *R. obtusifolius* populations ultimately changed to a phase with a decreasing probability of survival. In these two species, seasonal changes were unimportant to the overall population changes. That increasing environmental stress did not account for the decrease in the probability of survival was shown by an absence of a similar decrease in the probability of survival in younger plants.

The change in survival probability in the latter life stages of both of these species was associated with flowering in addition to the processes outlined above. It was not possible to determine from the available data whether repeated flowering caused the decrease in the probability or vice versa, or whether there was no causal connexion between the two.

(4) Contrasting Perennial Strategies

If the probability of survival decreases from year to year, the advantages of the perennial life history strategy cannot be continued indefinitely. Assuming that there are no environmental changes, the probability of survival only remains constant from year to year if the factors which were intrinsic to the development and growth of a plant do not affect this survival probability. In plants with cumulative growth of some axes, factors of scale sooner or later reduce the efficiency of various organs and the efficiency of the plant as a whole. The result of many life history tactics is to circumvent the inefficiencies resulting from factors of scale, or at least delay them.

As reproduction is principally associated with the plateau phase of the survival rate curve (and to a lesser extent with the third phase and its decreasing probability of survival), extensions of the plateau phase will result in longer periods of reproduction. Various habits and life histories result in an extension of the plateau phase in relation to the first phase of high mortality.

In some species, the production of auxilliary shoots etc. permits partial rejuvenation of the plant. This may be the case in redwoods, in which the production of sprouts at the base of the apparently senesced main trunk extends the plateau phase of the genotype (Bosch 1971). A second example may be found in some annual species which occasionally pass through to the second year (Primack, pers. comm.). A similar result is obtained in *R. crispus* and *R. obtusifolius* by limited peripheral root growth. As the plants become larger (and presumably the disadvantages of indeterminate growth are

manifest), the central root and shoots tend to die out as auxilliary buds develop, but the derivate plants probably have reduced lives compared to plants growing from primary axes.

In some species, the rejuvenation of plant parts is carried out more effectively. This is probably the case in *R. acetosella* where the adventitious root buds avoid the problems of indeterminate growth entirely. If each new adventitious root bud has the same probability of survival, the plateau phase of the whole genotype is extended indefinitely.

By morphological adaptations, the growing parts of other species are able to separate from the portions which become senesced and are thus rejuvenated indefinitely. The growth of certain rhizomatous plants and many grasses are examples of this type. In these species, the plateau phase of the whole plant is extended indefinitely.

In plants which circumvent senescence by the development of new buds, branches, etc., the original hump shaped probability of survival curve is repeated. However, the secondarily produced "unit" would have a hump shaped survival rate curve without the first part of the rise because they do not have to pass through a seedling stage. The combined plateau phases of the second and subsequently produced units results in the extension of the plateau phase for the whole individual. If the probability of survival of the secondarily produced organs was not as great as that of the "original plant", the probability of survival of the genotype would gradually decrease until the whole organism died (Fig. 30C).

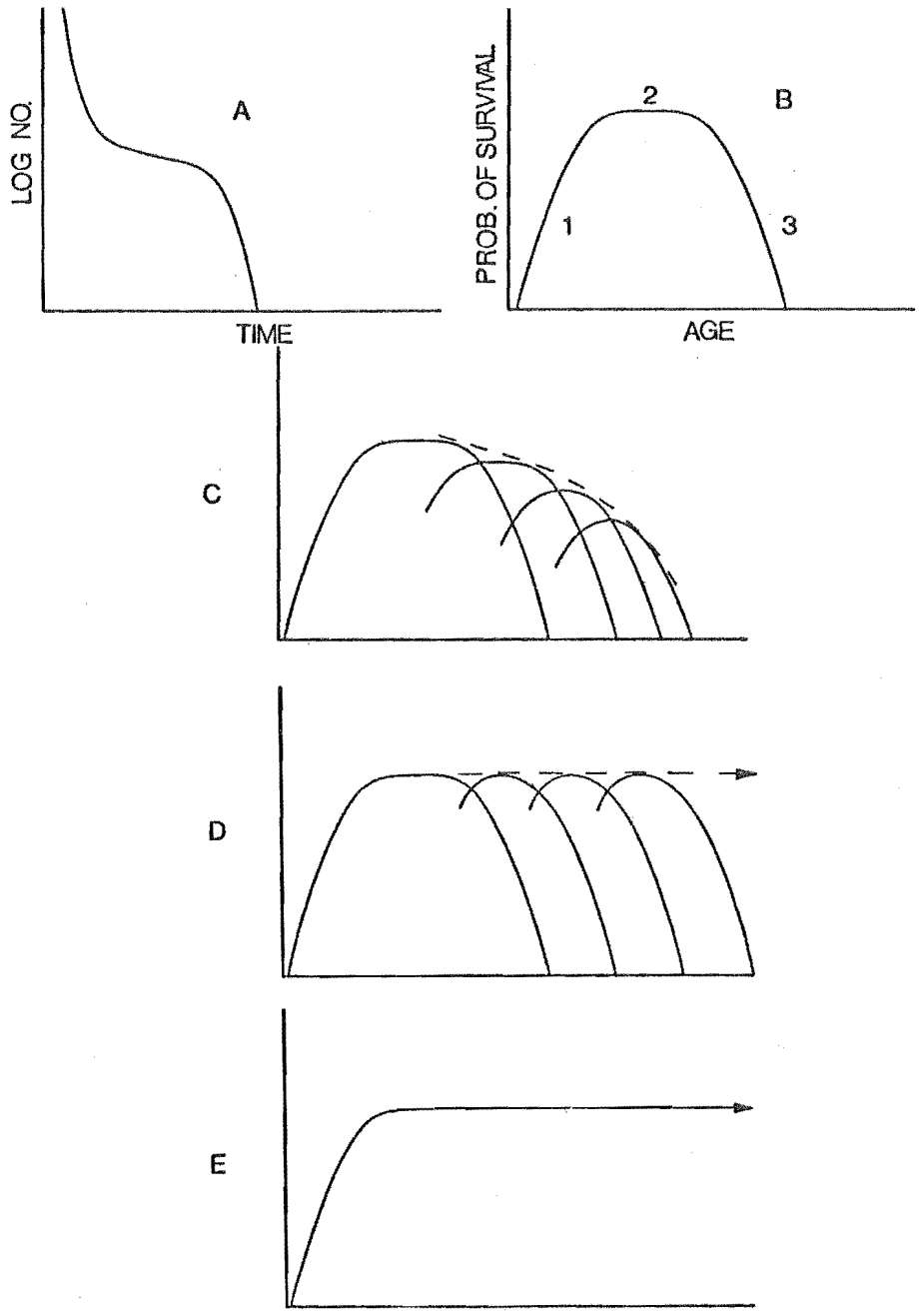


Fig. 30. Diagram showing survivorship and survival rate curves. A, concavo-convex survivorship curve. B, hump shaped survival rate curve. (1) Seedling or juvenile phase. (2) Plateau phase. (3) Senescing phase. C, D and E, see text for explanation. Dashed line shows the plateau phase for the genotype.

Species with the ability to continue the production of new units indefinitely are characterized by a series of hump shaped survival rate curves without the initial part of the first rise. If the product of the probability of survival of the vegetatively produced parts, and the frequency with which they are produced remains equal, the plant would be a "perpetual" perennial (Fig. 30D).

In species which rejuvenate themselves constantly, the survival rate curve would have an indefinitely extended plateau phase without a final decline (Fig. 30E).

Before an understanding of the mechanisms involved in the selection of life history strategies can be achieved, specific life histories must be described. Here the life histories of three *Rumex* species were related to the description of survival rates in successive intervals.

CHAPTER VI

A DISCUSSION OF THE ALLOCATION OF RESOURCES AND THE MECHANISMS OF REPRODUCTION

I. INTRODUCTION

Harper and White (1970) described a scheme illustrating the pathways concerned in the development of plant populations. Phase 1 represents the seed bank in the soil, most of which is dormant. Seeds are lost from the seed bank by germinating or by dying before they are able to escape dormancy. Phase II is the environmental sieve, representing the environmental constraints which prevent establishment of seedlings. The seedlings which are established grow and reproduce to varying degrees in phase III. The seeds produced may replenish the seed bank or germinate immediately.

Roberts (1970) outlined a scheme for the pathways involved in the dynamics of a population of viable weed seeds in soil. Mature plants from successfully germinated seed produce seed which may germinate immediately or suffer innate, induced or enforced dormancy. All stages are subject to mortality.

Here a synthesis of these two schemes is proposed which deals with the general and specific strategies and tactics of reproduction (both sexual and asexual), and their

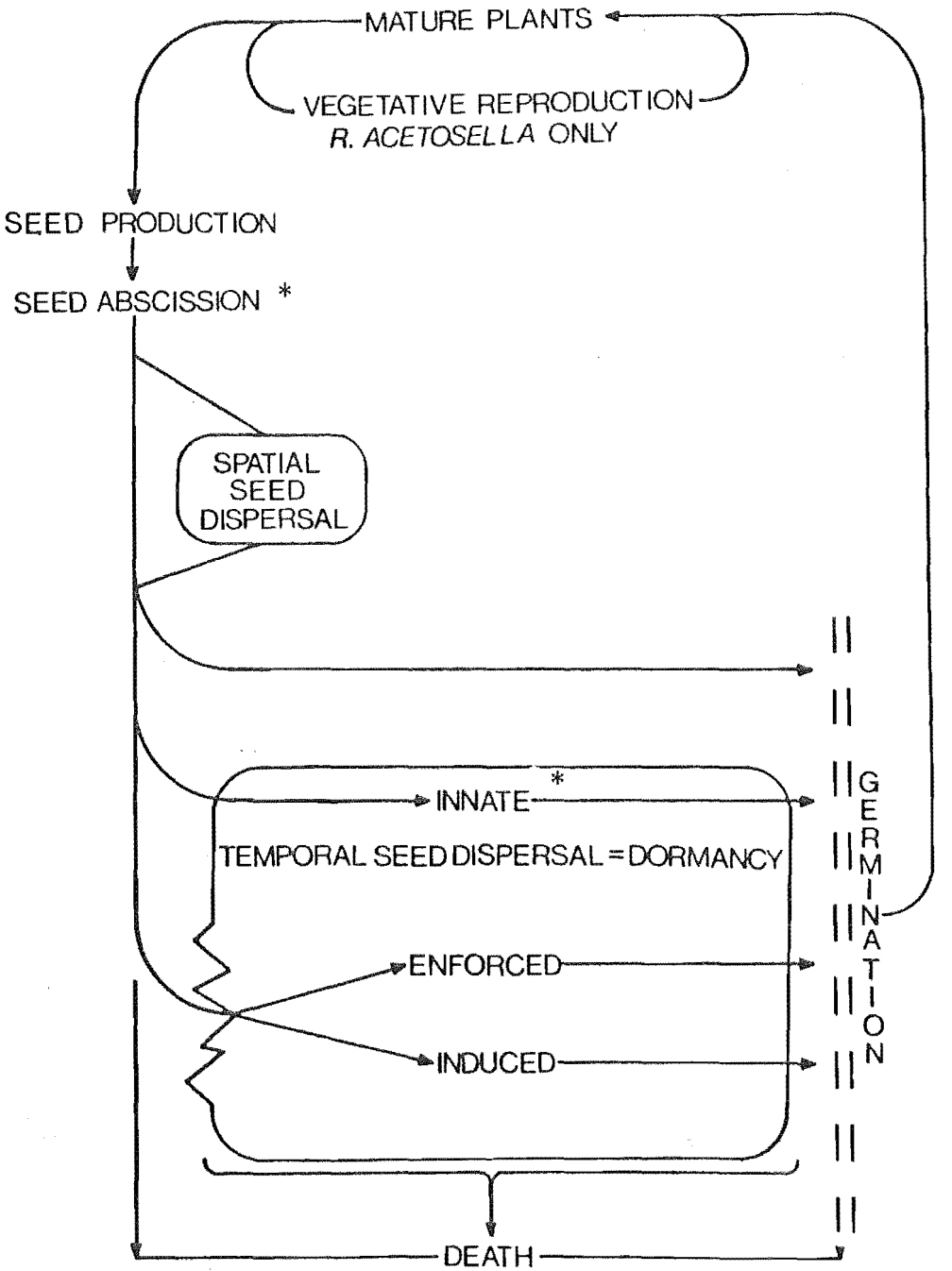


Fig. 31. Scheme illustrating possible pathways of various reproductive strategies.

* stages in which the plant can control germination time.

≈ = microsite differences

influence on population dynamics. The scheme includes vegetative reproduction, the amount of seed produced and the time of its abscission from the plant. The difference between seed which is spatially and temporally distributed and seed which is only distributed temporally is shown as well as the environmental factors which determine the type of dormancy regime suffered by various seeds (Fig. 31).

The discussion of the scheme is divided into two parts. The first of these is concerned with the allocation of resources to reproduction, and for *R. acetosella* the apportionment of resources between sexual and asexual reproduction. The second section is concerned with seed dispersal and the dynamics of soil seed. Each stage in the scheme is described and related to previous research and the results of this study. The adaptive significance of the various strategies is discussed and related to the general life history strategy of the species.

II. REPRODUCTIVE EFFORT IN EACH SPECIES

(1) Introduction

Cody (1966) suggested that the limited resources available to organisms are allocated in such a way that the contribution of the genotype to succeeding generations is maximized. Much of the recent interest in the allocation of resources, particularly to reproduction, has arisen from the concept of reproductive strategies introduced by Williams (1966), Tinkle (1969), Harper (1967) and Harper and Ogden (1970).

A limited variety of allocation patterns have been

described for plants growing at different densities, stress levels or successional stages. Harper and Ogden (1970) reported that *Senecio vulgaris* plants growing under two stress conditions did not differ significantly in their reproductive effort despite a seven-fold difference in mean plant size. Raynal and Bazzaz (1975) similarly found (on the basis of the number of seeds produced per gram of above ground vegetative tissue) that suppressed summer annuals (*Ambrosia artemisiifolia, Polygonum pensylvanicum* and *Seteria faberii*) did not allocate a greater proportion of their energy to reproduction than those which were not suppressed and although the reproductive allocation of *Taraxacum* (Gadgil and Solbrig 1972) and *Solidago* (Abrahamson and Gadgil 1973) varied among populations, it was fixed in any genotype.

In contrast to these results in which reproductive effort was fixed for the genotype or species, Hickman (1975) found that the reproductive effort of *Polygonum cascadense* was environmentally cued. The proportion of dry matter allocated to reproductive organs increased in harsher and more open habitats.

(2) Difficulties Associated with Measuring Resource Allocation

The estimation of shed tissues and the integration of multiple harvests make the estimation of organ costs difficult (Harper and Ogden 1970; Ogden 1974). In this study, tissue shedding resulted in the overestimation of absolute reproductive effort. However, trends in reproductive effort between species and populations were not affected.

The limitations of using energy determinations as a measure of plant organ cost have been pointed out by Harper and Ogden (1970) and Ogden (1974). The principal shortcoming of standing energy as a measure of total organ cost is that it does not account for respiratory construction and maintenance costs. Hickman (1975) has drawn attention to the dangers in the unsupported assumption that relative storage energy parallels relative respiratory costs. It has been assumed without foundation that the ratio of storage to respiratory cost is effectively constant for all products. It is the gross cost of organs which is subject to the force of natural selection. As it is currently impossible to assess the respiration construction and maintenance costs of organs, the results presented here only account for net stored energy.

(3) Reproductive Effort in *R. crispus* and *R. obtusifolius*

If the mean reproductive effort of all plants at each plot is considered, reproductive effort decreased with increasing plant density in both species. However, this was not due to lower reproductive effort by individual plants but to a lower proportion of plants which reproduced. The mean reproductive effort for plants which did flower was remarkably constant for both species at all plots. The maintenance of constant mean reproductive effort over a wide range of environmental conditions and plant densities parallels the results of Harper and Ogden (1970), Rynal and Bazzaz (1975), Gadgil and Solbrig (1972) and Abrahamson and Gadgil (1973) for a wide range of species. These results suggest that *R. crispus* and *R. obtusifolius* respond to

environmental and density stress by not flowering or flowering, and that once a plant is committed to flowering the range in which its reproductive effort must fall is genetically controlled.

The negative relationship within plots between total plant energy and modified reproductive effort (derived from the ratio of the energy allocated to reproductive organs divided by total root energy) suggested that although the overall range of reproductive efforts for each species is under genetic control, environmental cues determine the reproductive effort of individual plants within that range.

With the limited data available it is only possible to speculate on the negative relationship between modified reproductive energy and total plant energy within plots. It is possible that plants suffering adverse conditions resulting in smaller size are programmed to allocate proportionately more photosynthetate to reproduction whilst plants of larger size allocate more to vegetative organs. This may be a strategy permitting continued growth in favourable conditions, and greater reproductive effort in conditions likely to limit growth in the near future. Hickman (1975) suggested that the annual unpredictability of limiting resources is a strong selective force favouring plastic allocation of energy to seeds.

(4) Resource Allocation in *R. acetosella*

(a) Introduction: Harper (1967) stated that he knew of no attempts to compare the capital invested in seed and vegetative reproduction in any species that possessed both. He suggested that the partitioning of dry weight in plants

would make it possible to answer such ecological questions as: What is the relative energy expended in producing a seed and a vegetative propagule, and can this be related to the relative risk of establishment by the two means and the relative ecological importance of local and long range dispersal?

The experiments outlined here were a preliminary approach to these questions, and an attempt to discover which modes of reproduction would be favoured by *R. acetosella* plants under a variety of conditions.

(b) Sexual and vegetative reproduction in *R. acetosella:* In the field populations studied here, the extremely low rate of establishment by seed and comparatively high establishment rate by vegetative reproduction paralleled the results obtained by Putwain, Machin and Harper (1968) for *R. acetosella*, by Harberd (1961) for *Festuca rubra* and by Thomas and Dale (1975) for *Hieracium floribundum*. Thomas and Dale found that on the basis of "potential" reproduction, vegetative reproduction was 240 times more successful than sexual reproduction. Thus for the limited number of species studied so far, Harper's (1967) assessment of seeds as high risk and vegetative offspring as low risk propagules is borne out.

Attempts to measure the relative costs of seed and vegetative reproduction are complicated. There are methodological difficulties, not only in assigning gross costs to particular organs (as outlined above) but also in deciding the costs and contributions of organs ancillary to reproduction, for example, panicle leaves. With regard

to vegetative reproduction, the persistence of the connection between the parent and offspring and the photosynthetic tissue of the offspring makes it necessary to differentiate between photosynthetates from the parents and those produced in the offspring.

In *R. acetosella* it was found that the connexion between the parent and the offspring may persist indefinitely and that photosynthetate is translocated between parent and offspring in both directions for extended periods. However, the translocation of photosynthetate is disproportionately in favour of the offspring only during the early stages of offspring establishment. During these stages parents contribute 2000 times more photosynthate to offspring than vice versa. Once the offspring reach a dry weight of about 0.05 g, parents only contribute about three times more to offspring than vice versa. It is reasonable to presume that as offspring dry weight approaches parental dry weight, an equilibrium condition would become established. The mean proportion of parental resources that was expended on each vegetative offspring was 2.4%.

A crude estimate of the proportion of parental resources allocated to sexual reproduction was obtained by dividing the percentage of energy allocated to seeds and reproductive panicles by the total number of seeds produced in the treatment equivalent in stress to the radioactive tracer experiment. The mean percentage of a plant's resources expended on each seed was 0.04%. The mean allocation by plants to each vegetative offspring was therefore approximately 50 times the allocation per seed.

It should be emphasized that for the reasons outlined above, the "cost per seed" presented here is a crude estimate of the real cost.

It is not easy to measure the relative ecologic and genetic benefits afforded by sexual and vegetative reproduction. Some of these benefits have been discussed by Harper (1967, Abrahamson (1975) and Williams (1975).

Because vegetative and sexual reproduction differ in their ecological and genetical functions, it may be assumed that the relative advantages of each mode of reproduction alter, depending on the prevailing environmental conditions. It is possible to envisage that the allocation of resources to each mode of reproduction is adjusted in response to varying environmental conditions so that overall reproductive fitness is maximized.

Under stable conditions in a relatively closed community, the low mortality rates and "preselected" genotypes of vegetative offspring should be favoured. Under harsher and less predictable conditions, spatial and temporal dispersal of seedlings through seed reproduction might be favoured.

Under conditions of lower stress, greater *numbers* of seed, male flowers and vegetative offspring were produced. However, similar *proportions* of energy were allocated to male flowers and vegetative offspring under the three stress treatments. The proportion of energy allocated to seed production decreased as stress decreased. Thus, although the relative expenditure on vegetative reproduction was greater in the low than high stress conditions, this was only the result of adjustments in the allocation of

resources to seed. It appears that the allocation of resources to vegetative reproduction does not vary in response to environmental conditions. However, the increase in the number of vegetative offspring produced per unit of energy allocated to vegetative reproduction was disproportionately greater in the lower stress treatments. Thus, although the proportion of a plant's resources allocated to vegetative reproduction did not change with varying environmental conditions, the vegetative offspring produced by larger plants were smaller and proportionately more numerous.

(c) Reproductive effort in male and female *R. acetosella* plants: The increase in the proportion of resources allocated to seed reproduction in *R. acetosella* plants under harsher conditions (and therefore lower mean energy content) was similar to the within plot results for *R. crispus* and *R. obtusifolius*. The change in sexual reproductive effort with varying environmental conditions conformed to Hickman's (1975) prediction that plants should allocate more energy to reproduction under harsher conditions. Despite the increased allocation of resources to seed production, plants under harsher conditions still produce fewer seeds.

Because the allocation of resources to seed production decreased as conditions improved, whilst the allocation to male flowers remained constant with varying conditions, the ratio of reproductive effort in males to reproductive effort in females increased as conditions improved. This is similar to the results evident in Figure 4 of Putwain and Harper (1972) for the number of

inflorescences borne on male and female *R. acetosa* plants. As plant dry weight increased, the proportional production of inflorescences by females decreased at a greater rate than the production of inflorescences by males.

As the effectiveness of male reproductive effort is limited by available ovule numbers, the production of pollen beyond saturation level does not increase male reproductive fitness. It is probable that because of the low cost of pollen, pollen production can be maintained at saturation levels under harsh conditions without increased male reproductive effort (Lloyd and Webb in press).

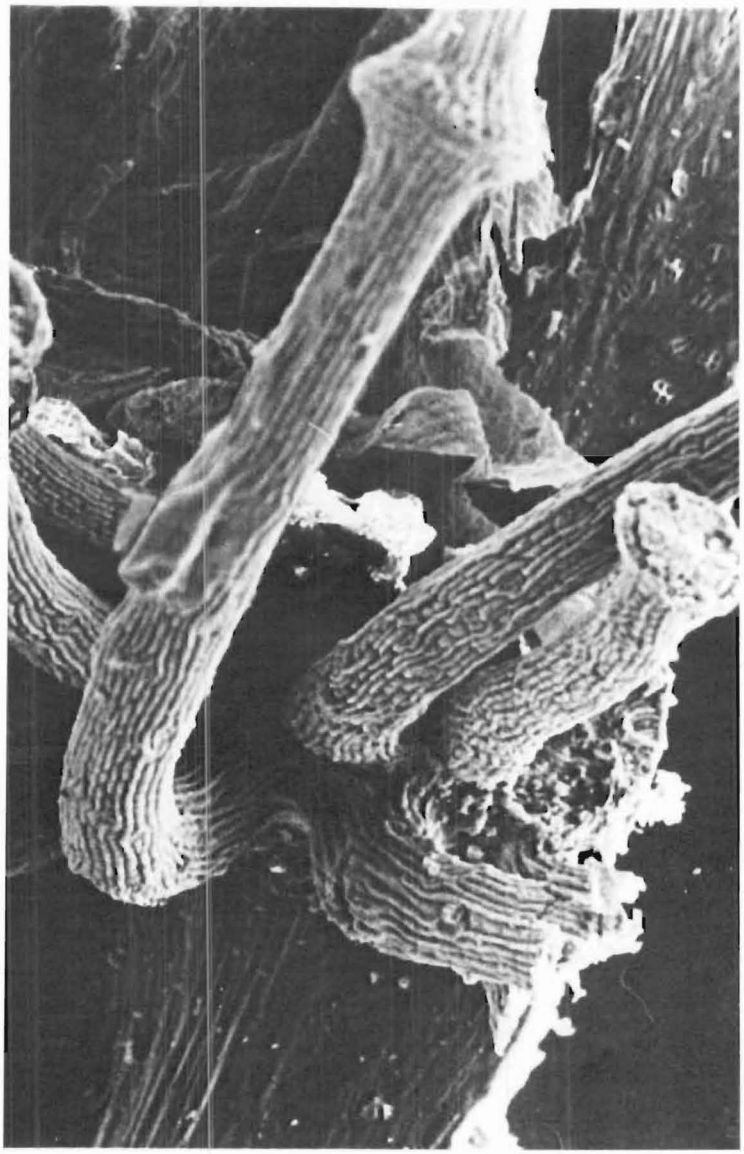
III. SEED ABSCISSION

(1) Introduction and Possible Significance of Seed Abscission

A period of rest intervenes between seed maturation and germination (Harper and White 1974) which allows for seasonal adjustment of the time of seedling germination and establishment.

There are only two stages after the production of seeds in the scheme where the three species involved have a degree of direct temporal control. These are the time at which seed abscission takes place and the period for which seeds are innately dormant. In *R. crispus* and *R. obtusifolius*, seed abscission is accomplished by the fracture of a distinct zone of the pedicel . *R. acetosella* does not have an abscission zone. The significance of the abscission zone and its potential for the temporal control of seed drop is not generally appreciated. Cavers and Harper (1964)

Plate 6. *R. crispus*. A portion of the panicle showing the origin of a number of pedicels . The point at which the pedicels are inserted is buttressed and heavily ribbed. (× 80).



mentioned that sporadic germination is assured since the fruits drop from the inflorescence throughout the late summer, autumn and winter. In referring to *R. crispus*, Maun (1974B) described fruit dispersal as starting about a month after seed maturity and continuing until next spring. In Ontaria, a large number of seeds overwinter on the flower stalk.

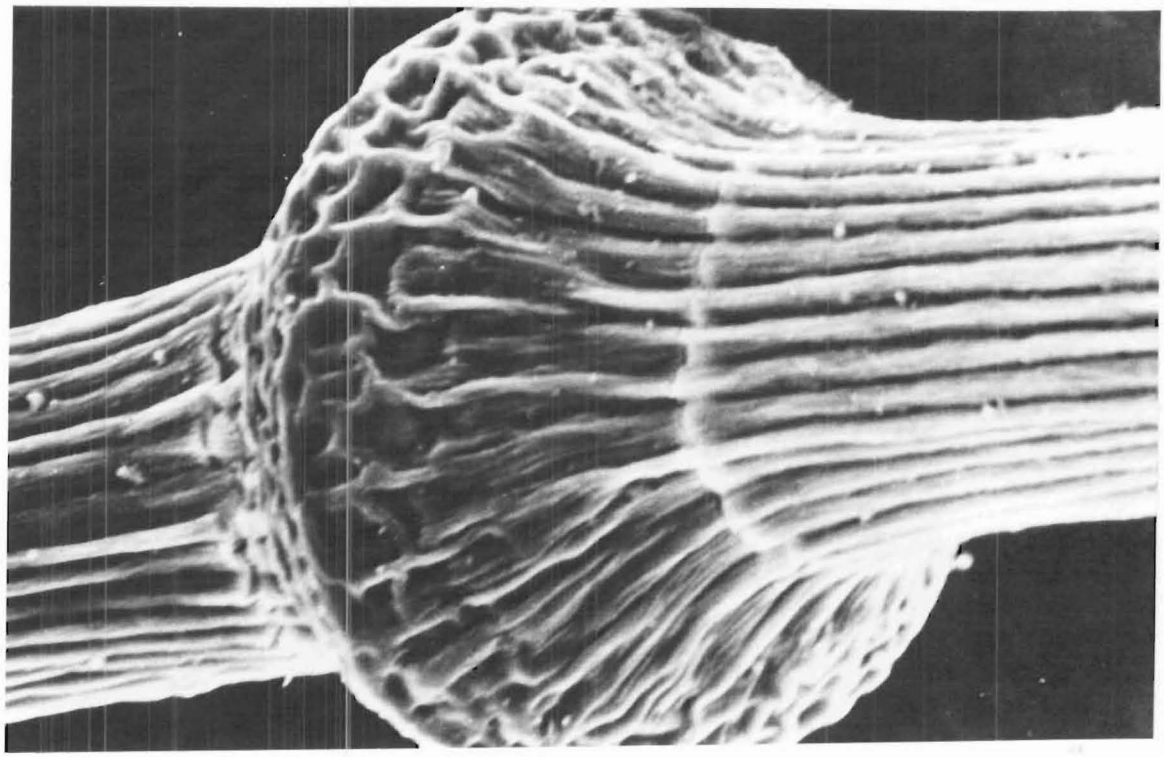
I noticed that *R. acetosella* could be made to drop a large proportion of its seed by gently tapping the panicle, whilst for *R. crispus* and *R. obtusifolius* vigorous movement would only result in a few seeds being shed from the panicles. In nature, *R. acetosella* plants usually lose all their seed within a very short time. The other two species retain most of their seeds on the panicle for some months after they have matured and often until the beginning of June. By the end of July only a few seeds remain on the panicle. Some seeds overwinter on the panicle, and in very sheltered areas may remain on the panicle beyond the next fruiting season. This does not often happen on agricultural land as the panicles are usually damaged by stock, mowing or cultivation.

(2) Abscission Zone Structures in *R. crispus* and *R. obtusifolius*

The pedicel structure in *R. crispus* and *R. obtusifolius* suggests that it is strengthened to resist fracture at any point except the abscission zone. In both species the pedicel is buttressed at its base, where the leverage is greatest (Plate 6). The whole pedicel is extensively ribbed in *R. crispus* and covered with reticulated thickening

Plate 7. *R. crispus* pedicel and abscission zone.
The pedicel is covered with longitudinal, thickened ribs.
(× 360).

Plate 8. *R. obtusifolius* pedicel and abscission zone.
Reticulated thickening covers the whole of the pedicel .
(× 430).



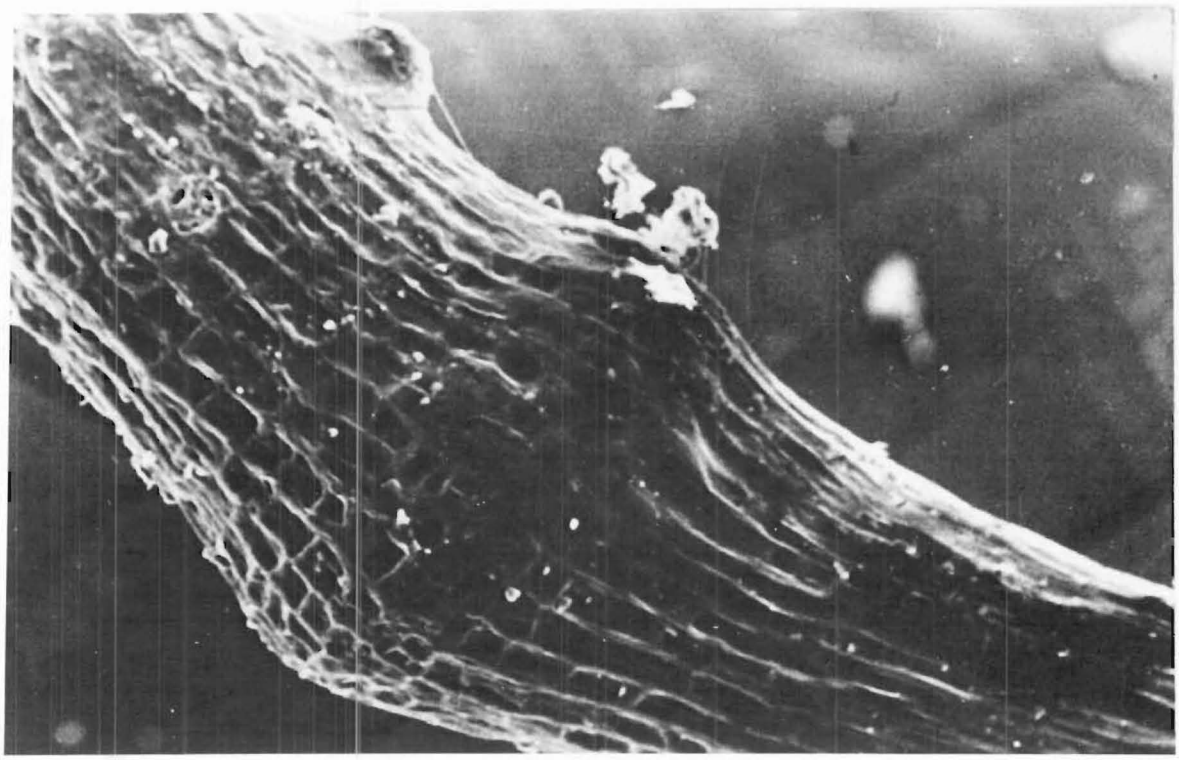
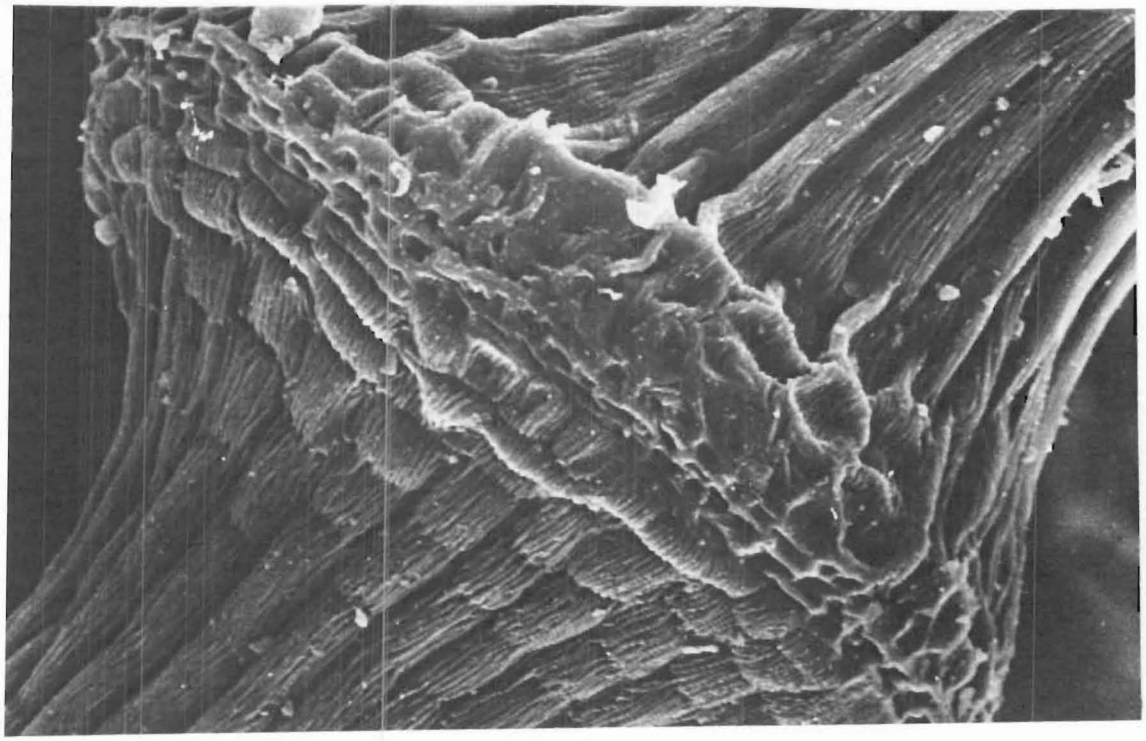
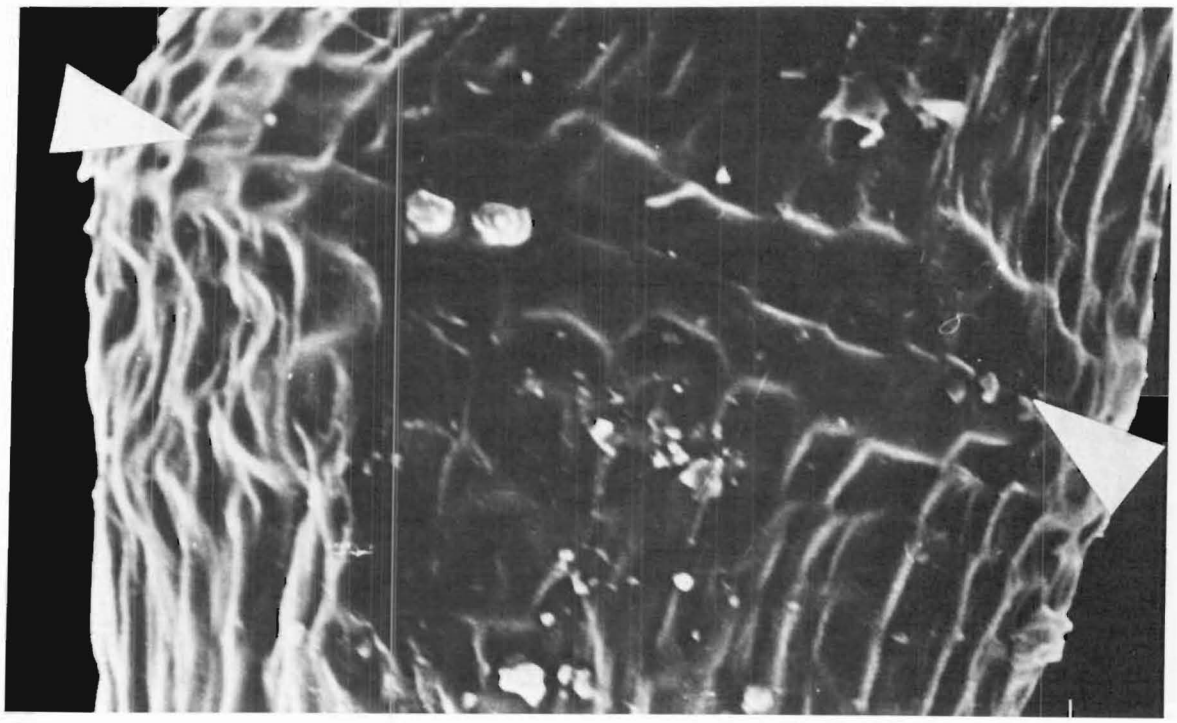


Plate 9. *R. crispus* abscission zone. The ribbing on the abscission zone is interrupted by a thin band of reticulated thickening. (× 830).

Plate 10. *R. obtusifolius* abscission zone. The reticulated thickening on the pedicel is interrupted by a smooth edge bordering the comparatively unthickened abscission zone. (× 900).





In *R. obtusifolius* (Plates 7 and 8). The lignification of these tissues also contributes to pedicel strength.

The external morphology of the abscission zone and the surrounding area in the two species is strikingly different.

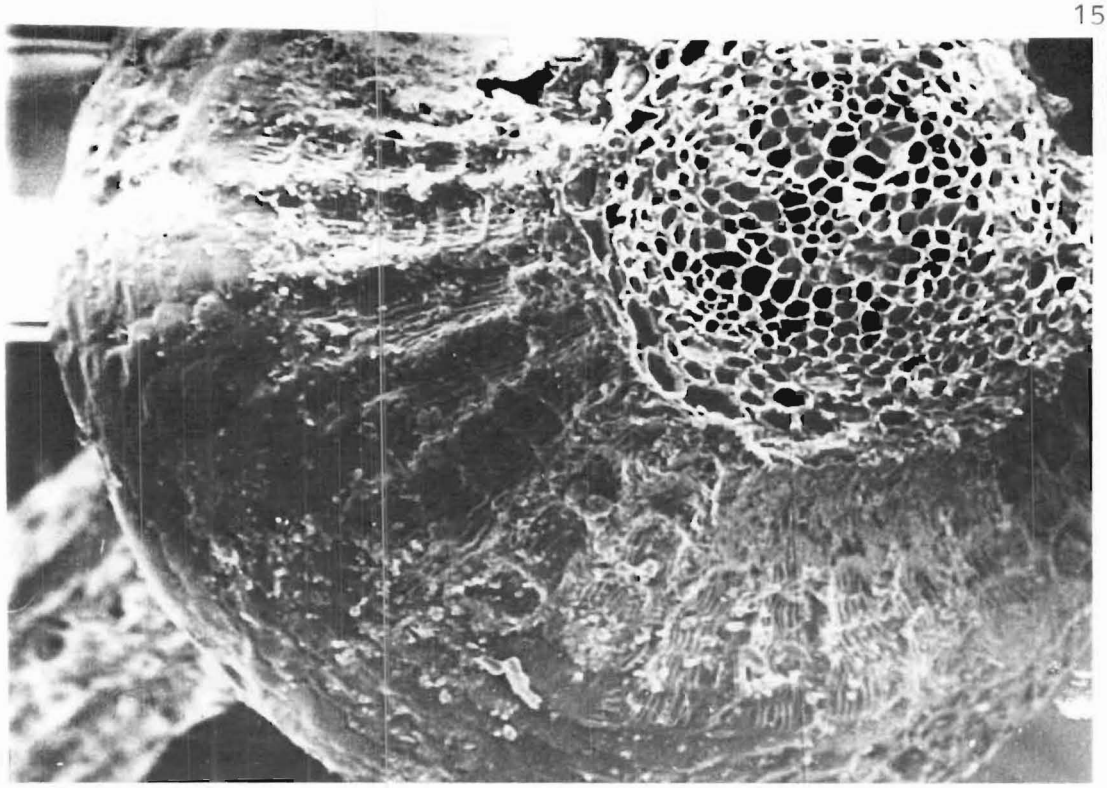
In *R. crispus*, the abscission zone is almost twice as wide as the pedicel and appears as a thin band of fine, reticulated thickening which interrupts the peduncle ribbing (Plate 9). In *R. obtusifolius*, the abscission zone is in a slightly swollen area of the pedicel and appears as a thin band without thickening (Plate 10). Seed release takes place by the fracture of the abscission zone.

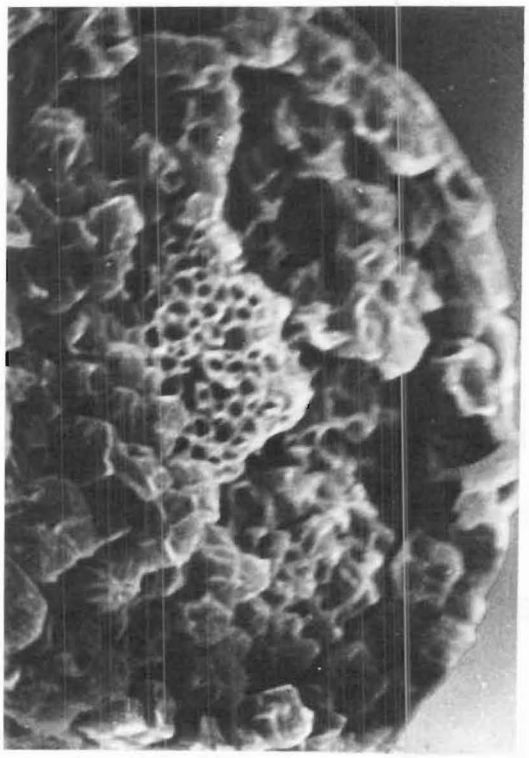
The position of the abscission zone differs in these species. The ratio of the abaxial half of the pedicel to the adaxial half is 0.75 in *R. crispus* and 0.68 in *R. obtusifolius*. Thus the mechanical advantage acting on the abscission zone in *R. obtusifolius* is slightly higher than in *R. crispus*. This will further weaken the effective strength of the abscission zone in *R. obtusifolius*.

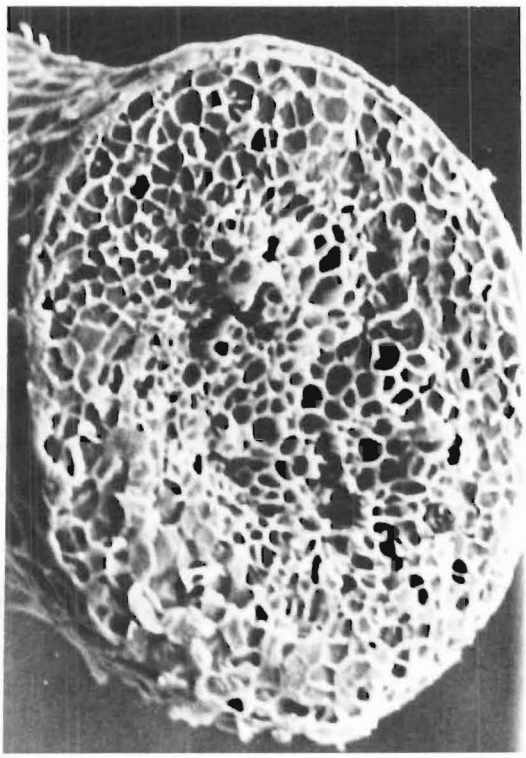
Initially, the strength of the abscission zone is far higher than that of the pedicel. If the seed is forcibly removed, the pedicel rather than the abscission zone will fracture, as shown in Plate 11. If the abscission zone is broken at this stage it will tear rather than fracture (Plate 12). Some time after seed maturity the abscission zone undergoes a change, making it weaker than the pedicel. After this change the abscission zone will fracture cleanly (Plate 13).

Plate 11. *R. crispus* fractured pedicel . The abscission zone has remained intact, whilst the pedicel has fractured. (× 370).

Plates 12 and 13. *R. obtusifolius*. In Plate 12, the abscission zone has been artificially torn apart before it has weakened, leaving an uneven, ragged surface. (× 720). Plate 13 shows the smooth, relatively even surface of an abscission zone which has weakened and come apart naturally. (× 650).





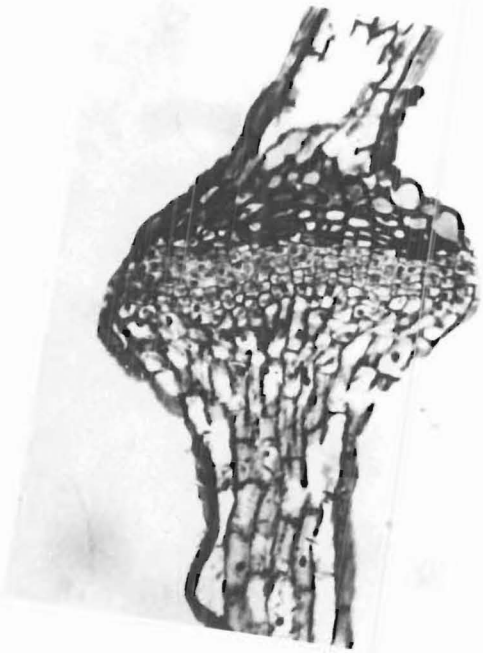


Plates 14 and 15 show the abscission layer in *R. crispus* approximately 2 and 4 months after seed maturity respectively. (× 130) (× 130).

See Chapter IV under Seed Fall and Abscission Zone Structure for explanation.

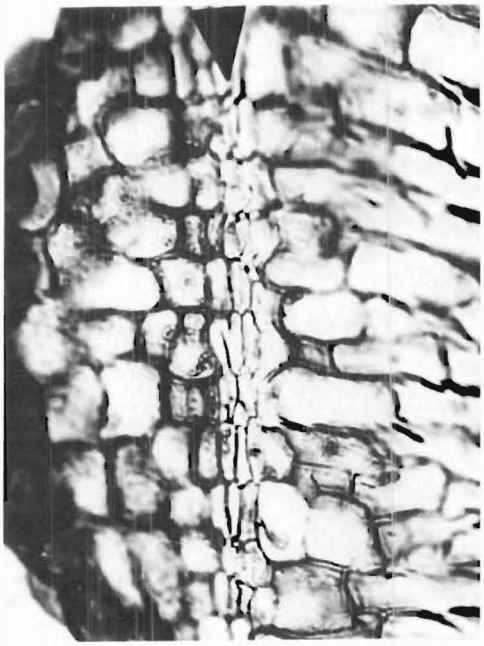
Plate 16. *R. crispus*, abscission zone approximately six months after seed maturity. By this time almost all of the cells in the abscission zone have collapsed completely. (× 280).

See Chapter IV under Seed Fall and Abscission Zone Structure for explanation.



Plates 17 and 18. *R. obtusifolius* abscission zone.
In Plate 17 the abscission zone consists of a layer about 3 cells wide approximately 2 months after seed maturity. (× 600). Four months after seed maturity some of the cells have started to break down (Plate 18). (× 250).

See Chapter IV under Seed Fall and Abscission Zone Structure for explanation.



(3) The Demographic and Ecological Significance of Controlled Abscission Zone Fracture

Harper and White (1974) asserted that seasonal dormancy is demographically unimportant except where a pause in the life cycle slows down the potential rate of population increase. However, if seasonal dormancy alters the probability of seed surviving to establishment, it may alter the effective reproduction of the parent. The advantages accruing from improved dispersal and finer temporal control over the time of germination may result in higher rates of establishment despite the resultant pause in the life cycle.

The retention of the seed on the panicle effectively enforces dormancy on the seed for a minimum time which can be controlled by the parent plant. The time at which the abscission zone weakens and thus allows seed dispersal to take place is adaptively significant.

Seed borne on the panicle is in a less hazardous environment than soil seed because it is not subject to predation by soil dwelling animals or damage by micro-organisms. Furthermore, it is more likely to be picked up by man, animals or machinery or to be dispersed by wind when it is on the panicle than when it is on the ground.

IV. SPATIAL SEED DISPERSAL

(1) Introduction

When the dispesal characteristics of these three species are considered, one fact is striking. This is the enormous number of seeds which fall immediately at the foot of the reproductive panicle. *R. crispus* and *R. obtusifolius*

plants which are dropping seed frequently have a layer of seeds up to a few millimetres deep on the ground within the shoots of the plant. The behaviour of *R. acetosella* is similar, although not quite so apparent because the seeds are much smaller and become buried or lost to sight more easily. Thus it seems that the effective dispersal of these species must be carried out by the remaining small proportion of seeds which do not fall at the foot of the parent plant. This agrees with Levin and Kerster's (1974) observation that the spatial dispersal of a majority of windborne seeds is restricted.

Cavers and Harper (1964) have described the dispersal of *R. obtusifolius* seeds as being by wind, water, adhering to the fur of animals (in mud or with the perianth teeth), or internally in the digestive system of cows. They describe a similar situation for *R. crispus*, stressing the ability of the seeds to float with the aid of corky tubercles on the perianth segments. Healy (1969) has classified the seeds of *R. acetosella* as being of a type which secrete mucilage and are consequently able to adhere to animals. This has not been confirmed by my observations.

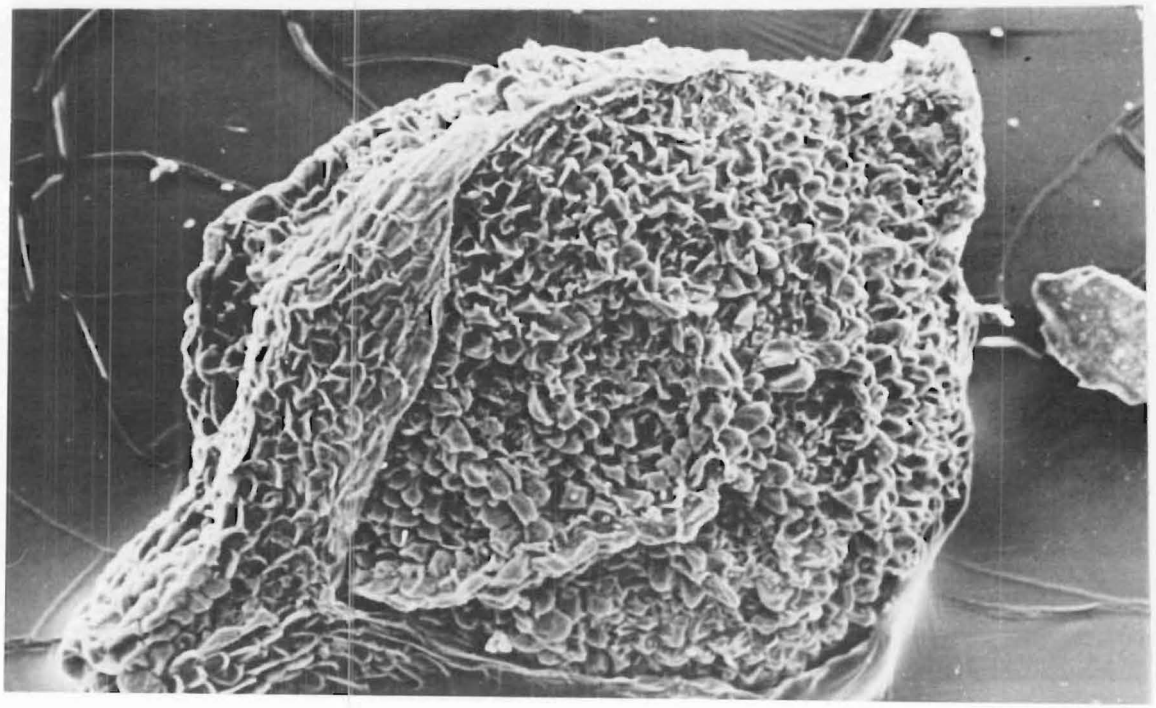
(2) The Effective Dispersal Units of the Species

The effective dispersal unit of *R. acetosella* is the fruit enclosed by three closely adherent perianth segments.

The pedicel usually breaks at the junction between it and the seed, leaving only the sepals attached to the seed. The naked seed cannot be removed from the perianth segments. (This is the angiocarpic seed state described by Harris (1969).) Each of the perianth segments covers

Plate 19. *R. acetosella*. The fruit and enclosing perianth segments which are dispersed as a whole. The pedicel has broken off near the seed. (× 60).

Plate 20. *R. acetosella*. The apex of the seed showing the bulbous projections which cover the perianth segments. (× 300).



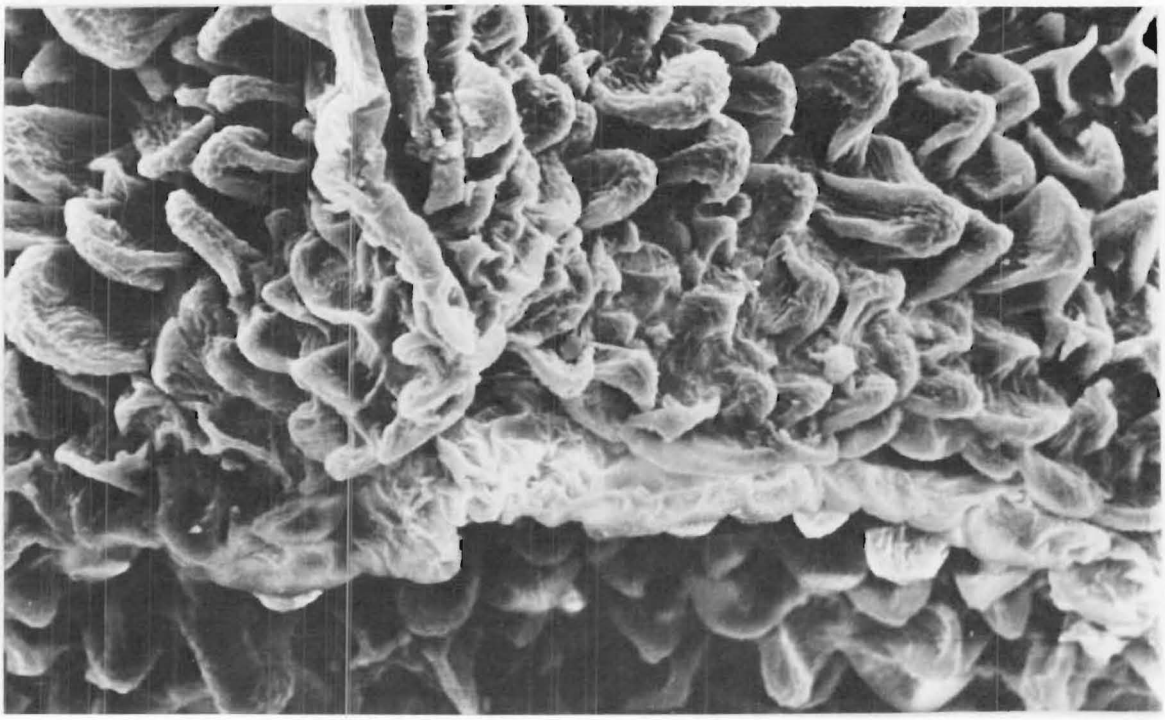
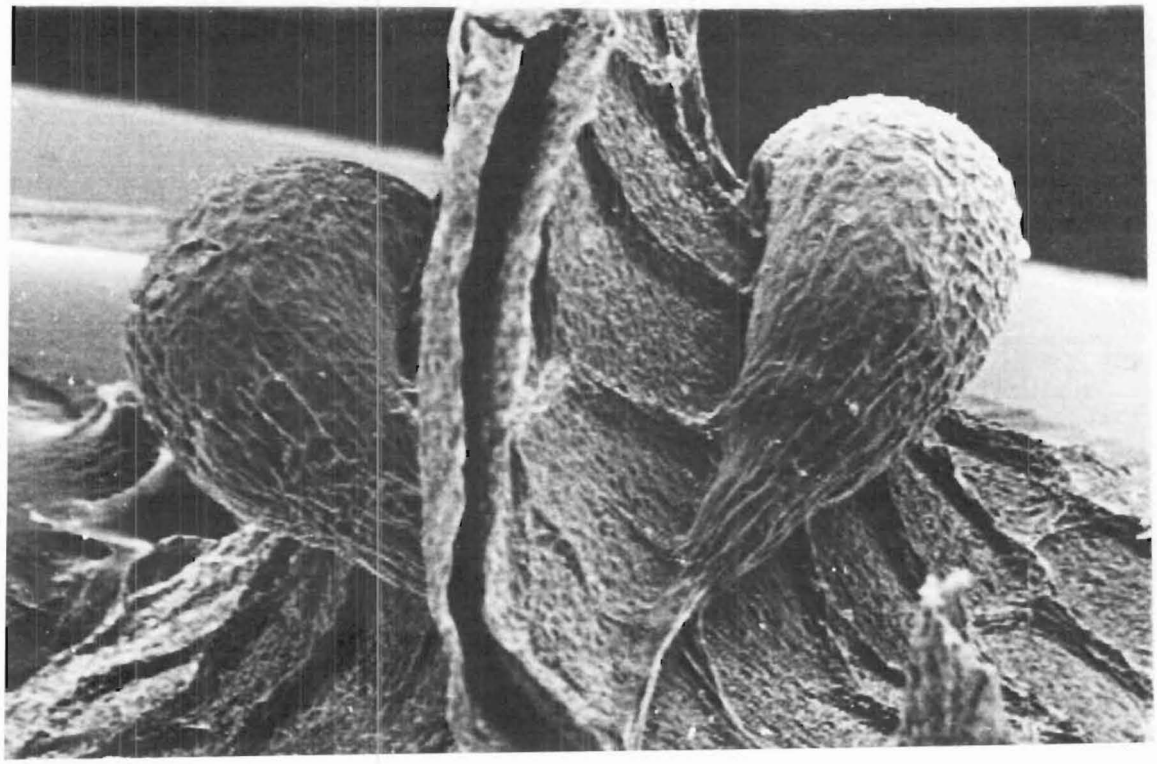
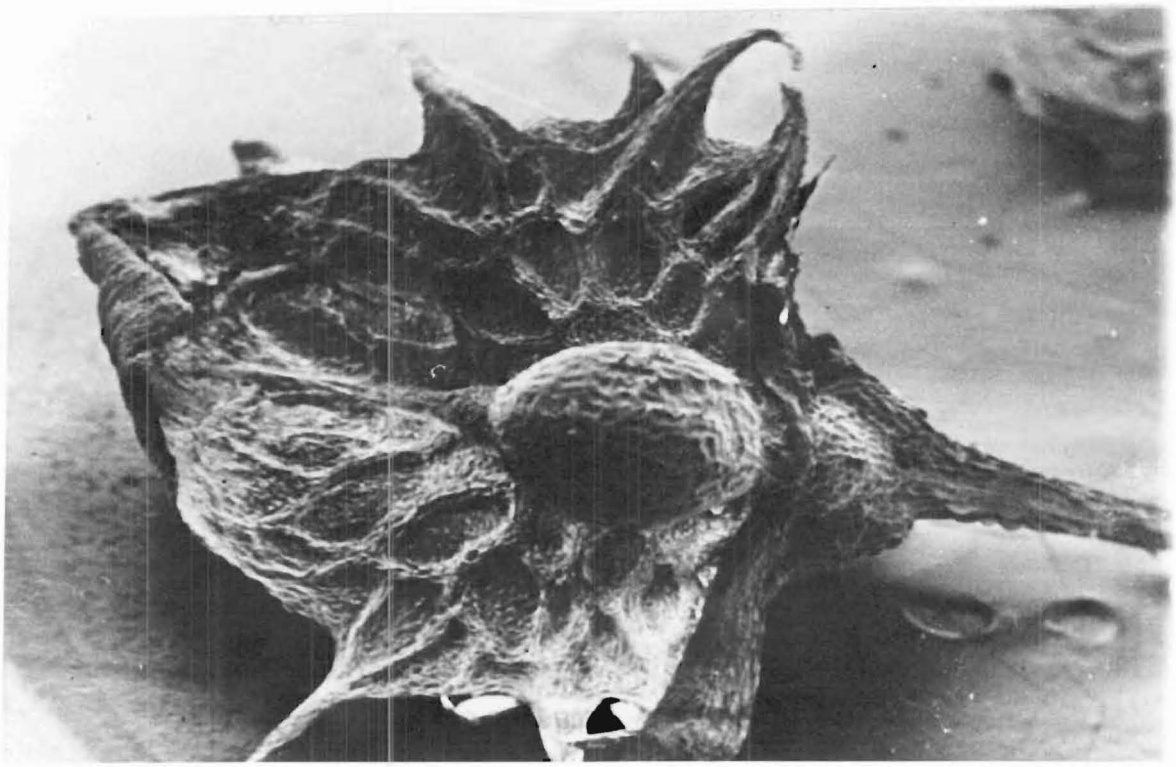


Plate 21. *R. crispus*. The seed, enclosed by smooth-edged valves. The valves usually have one well-developed tubercle (shown on the left) and two less well-developed tubercles. (× 240).

Plate 22. *R. obtusifolius*. The seed is enclosed by toothed valves, some of which are hooked. One less well-developed tubercle is shown. (× 25).





one of the three curved surfaces of the seed, which are covered with a multitude of bulbous projections (Plates 19 and 20). There appear to be no special modifications for attachment or flotation, although the bulbous projections on the perianth segments may contribute towards the buoyancy of the seed in air. Their function is otherwise unknown, although they are photosynthetic in the early stages of seed development.

The dispersal unit of *R. crispus* seeds consists of the seed which is of a similar shape to that of *R. acetosella* but slightly larger (about 2.4 mm long and 1.4 mm wide) and three perianth segments. The perianth segments are extended to form large valves with smooth edges (Plate 21). One of these was a well developed, corky tubercle, whilst the other two valves usually bear a similar, but reduced tubercle of about half the size. The pedicel usually remains attached to the perianth segments. Generally the seed is dispersed in this form, but it may be mechanically dislodged from its enclosing perianth segments by mowing, cultivation, etc.

R. obtusifolius seeds are also usually dispersed in their enclosing perianth segments. In this species, the perianth segments are also extended, but not smoothly as in *R. crispus*. In *R. obtusifolius* the perianth segments have teeth along their margins, which often exceed the width of the segments in length and are sometimes hooked at their ends (Plate 22). Usually only one of the perianth segments bears a well developed tubercle, although one of the other two tubercles may be partially developed. The pedicel usually remains attached to the perianth segments.

The perianth segments of all three species are photosynthetic and easily wettable. Apart from elevating the seeds above the ground, the plants do not contribute to the dispersal of the seeds.

(3) Means of Dispersal

(a) Wind: Large numbers of seedlings are usually found close to the parent plant, reflecting a leptokurtic distribution of seeds. The distance that seed is dispersed is related to the presentation height. In work with *Senecio jacobaea*, Sheldon and Burrows (1973) found that the distance travelled by the achene plus pappus was almost directly related to the presentation height.

However, panicle elevation may also increase the competitive ability of the photosynthetic organs borne on the panicles, as well as contributing to seed dispersal.

Although a casual inspection of the enclosing perianth segments on the seeds of *R. crispus* and *R. obtusifolius* would suggest that the seeds of the former might be better adapted to being carried by wind, wind tunnel tests have shown no difference. Levin and Kerster (1974) stated that the distance seeds travel is influenced by settling rate, the height and area of the source, turbulence and wind velocity. In the wind tunnel test, turbulence was minimized whilst wind velocity and release height were kept constant. Thus the distance travelled by each seed was proportional to its settling rate or sink velocity. Other things being constant, the distance a seed travels is directly related to wind speed. The mean distance travelled by seeds were not significantly different in the

two species in wind tunnel tests. The mean distance travelled by *R. acetosella* seeds was not significantly different from the distance travelled by seeds of the other two species either. However, the maximum distance travelled by any seed was 50% further for *R. acetosella* than for *R. crispus*. This is associated with the voilure index (the area of the seed in square centimetres divided by its weight in grams) which is 39 for *R. crispus* and 84 for *R. acetosella*. (King 1966, from Hitrovo 1912. As Hitrovo's original paper was not available, I was unable to determine whether these measures referred to the naked seeds or the seed and the enclosing perianth segments.) Once *R. acetosella* seeds have been picked up by the wind they probably travel further than the seeds of the other two species. Levin (1973) stated that wind is the most significant means of dispersal for lighter seeds. However, unless the winds carrying the seeds are much stronger than normal, the distances over which the seeds of all three species are transported is probably only a matter of a few metres. Maun (1974B) also pointed out that the seeds of *R. crispus* do not travel far from the parent as they possess no special modifications for wind dispersal. The abscission zone may ensure that seeds of *R. crispus* and *R. obtusifolius* are only dislodged from the panicle by stronger winds than those prevailing normally. In these two species, the seeds are held on to the panicle relatively firmly; thus only above-average winds are able to dislodge seeds. The seeds of *R. acetosella* are not held on to the panicle so firmly and are easily dislodged. Wind dispersal is not the most frequent means of dispersal for the seeds of

these species, although a few seeds, particularly those of *R. acetosella*, may be carried over long distances during extremely strong winds.

(b) Water: The ability of the seeds of the three species to remain floating in agitated water is remarkably different. Because most *R. acetosella* seeds sink immediately it is not likely that they are adapted for dispersal by water. It is probable that the seeds of both *R. crispus* and *R. obtusifolius* are often dispersed by water; in both cases the buoyancy is principally provided by the tubercles. Both species frequently inhabit land prone to flooding and areas adjacent to moving water. Seeds must often fall from the parent plant to be carried away by moving water or be picked up after falling on to the ground by advancing flood water. Evans (1968) stated that the dispersal of *Rumex* seeds by winter rains from ditches, hillsides and woodland areas or by flooding contribute to their being a perennial problem to farmers. The distribution of *R. crispus* and *R. obtusifolius* plants at the site of plots 1 and 6 is an example of this kind of dispersal. After initial establishment in the field by some plants of both species, seedlings from these plants have grown in the area which becomes flooded each year. That the dispersal of seeds by the flood water rather than a preference of the plants for flooded areas accounts for the distribution of the plants in that particular field is suggested by the presence of plants in nearby areas which are not prone to periodic flooding. The distribution of both of these species over long distances is likely. For example, using a Watts current meter, a mean flow speed of

0.541 m/sec was computed from bank and centre measures for the Waimakariri River when it was neither low nor in flood. At this rate of flow, it would take a seed about 40 hours to travel from the headwaters of the river to the sea, a distance of 136 km. Over this time, more than 90% of the *R. crispus* and *R. obtusifolius* seeds would still be floating.

The germination response of *R. crispus* and *R. obtusifolius* is related to their reliance on water dispersal. *R. crispus*, which relies on dispersal by water to a greater extent than *R. obtusifolius*, gave very low germination percentages when it was submerged (7%). In this situation the germination of seeds was strongly inhibited. The ability of seeds which are commonly dispersed by water to germinate whilst submerged is almost certainly maladaptive. A smaller percentage of *R. obtusifolius* seeds (20%) resisted germination whilst submerged. This is possibly explained by the decreased reliance of this species on water dispersal. The relatively low germination percentage of submerged *R. acetosella* seeds (13%) is not indicative of its relative dependence on water dispersal, as this species is not found on waterlogged soil or areas subject to flooding. The percentage of *R. acetosella* seeds germinating under water is most likely to be related to other requirements of germination.

(c) External dispersal on animals: The remaining means by which seeds of these three species can be dispersed must depend on transportation by birds, man or other animals.

The adherence of *R. acetosella* to *R. crispus* seeds to either birds or mammals is not likely, as the seed of neither

species bears any projections or mechanisms by which the seed or perianth segments might adhere. The attachment of *R. obtusifolius* seeds to animal fur, clothing, or possibly birds is much more likely, especially from their elevated position on the panicle. The teeth of the perianth segments, especially those that bear hooks, easily become entangled in fur or clothing. A preliminary experiment in which seed was dropped from 5 cm on to a 40 cm long plane inclined at 45° and covered in finely knitted wool supported this conclusion. Only 2% of the *R. acetosella* seeds stopped on the inclined plane, compared to 16% for *R. crispus* and 78% for *R. obtusifolius*. The attachment of the perianth segments of *R. obtusifolius* is not strong, and seeds are easily dislodged. I have observed *R. obtusifolius* seeds attached to the coats of farm dogs in this manner.

(d) Internal dispersal by animals and birds: Seeds which are dispersed after ingestion by birds or animals must be capable of surviving in the gut and must be evacuated into a suitable environment for germination.

Cavers and Harper (1964) refer to an account by Amphlett and Rea (1909) which states that *R. crispus* and *R. obtusifolius* are refused by cattle, sheep and horses although they are eaten by deer. However, I have observed sheep eating plants of both these species and *R. acetosella*. Salisbury (1961) has found seeds of *R. crispus* and *R. obtusifolius* in cattle droppings, and I have observed them in horse faeces. Thus it is likely that the unintentional ingestion of seed of all three species by farm

animals is common.

The ability of *R. crispus* and *R. obtusifolius* seeds to survive in the digestive tracts of cows (Salisbury 1961) and horses has been established. Salisbury (1954) includes docks among a list of weeds whose germination rate may be increased after passage through cows. In an extensive experiment by Harmon and Keim (1934), the percentage survival of *R. acetosella* seeds ingested by calves, horses, sheep and hogs was determined. Although an average 8% of seeds survived ingestion and could be recovered from these animals, none could be recovered after ingestion by chickens. Cooper, Maxwell and Owens (1960) also found that no dock seeds (species not stated) were passed by chickens. Of the seeds which were fed to these animals, an average of 5.1% remained viable. I have not seen birds eating the seeds of these three species.

Although *R. crispus* and *R. obtusifolius* seeds were able to survive burial in manure for some time (Cavers and Harper 1966), *R. acetosella* seeds were unable to survive for one month in either cow or horse manure (Harmon and Keim 1934).

(e) Dispersal by man on machinery and in seed crops: Man is probably directly responsible for a large proportion of the dissemination of *R. crispus* and *R. obtusifolius* seeds. Salisbury (1954) thought that this was of greater significance in weed dispersal than the external carriage of seed by stock. Seed is dispersed on clothing and in soil and mud adhering to shoes, vehicle tyres and farm machinery. The most troublesome form of dispersal for agriculture occurs in crop seed and hay. Plants growing from seed

dispersed by this means become established and grow in a crop they have successfully competed amongst on previous occasions. Healy (1969) suggested that all three species of *Rumex* were probably introduced to New Zealand as impurities in crop seed. Salisbury states that up to 40,000 weed seeds per acre are unwittingly disseminated in crop seed. As *R. crispus* frequently ranks amongs the five commonest contaminants of crop seed, the number of its seeds which are distributed must be very large. It is probable that *R. acetosella* and *R. obtusifolius* are similarly disseminated.

As methods of cleaning crop seeds improve, the selection for weed seeds which are similar to those of the crop becomes stronger.

(f) Ecological and reproductive considerations of dispersal: When the long range dispersal of weeds is being considered it is also necessary to know whether a single weed can establish a population capable of producing more seeds (Salisbury 1954). If more than one plant has to be established in an area before seeds can be produced, the chances of successful and lasting long range dispersal are decreased enormously (Baker 1955).

R. acetosella is a dioecious species and thus requires the presence of a plant of the opposite sex within the distance over which pollen can be dispersed effectively. However, because of the capability of a single plant to colonize a large area by vegetative means, and the perennial nature of the genotype, a single seed could produce a large colony of plants. Such colonies would be able to survive for

extended periods until a plant of the opposite sex became established within pollinating distance.

The ability of *R. crispus* plants to fertilize themselves is disputed. Cavers and Harper (1964) state that the self-fertility of the inland varieties varies between 25 and 100% in Caernarvonshire plants. Mulligan and Findlay (1970) found that the Canadian *R. crispus* plants they studied were incapable of self fertilization. Most *R. obtusifolius* plants are highly self fertile (Cavers and Harper 1964). Thus it is likely that a large proportion of *R. obtusifolius* plants are capable of establishing a localized population from one seed.

In conclusion, localized or primary distribution (in the sense used by Salisbury 1954) is commonly carried out naturally or by the accidental intervention of domestic animals and man. Long range or secondary dispersal of the three species is probably different, *R. acetosella* being dispersed over long distances less often than the other two species. All three species are dispersed over great distances by a variety of agricultural practices, principally as contaminants in crop seed.

V. THE FATE OF SEED FALLING TO THE SOIL SURFACE

(1) Introduction

Seeds may germinate or become dormant as soon as they fall from the plant or after spatial dispersal has taken place. Dormant seeds which escape death are temporally dispersed. There are three kinds of dormancy (Harper 1975A). Seeds may be innately dormant and require the passage of a

certain time or the presence of certain environmental conditions before they will germinate. Seeds with induced dormancy are able to germinate immediately, but because of some environmental factor their germination requirements are modified. Such seeds will not germinate until certain temporal or environmental conditions are met. Seeds which suffer enforced dormancy (e.g., by deep burial) will germinate freely when the conditions enforcing their dormancy are removed. However, the seeds must be physiologically capable of surviving the extended periods over which germination is prevented. Seeds which have been innately dormant or have had dormancy induced in them may be released from these restraints into a condition of enforced dormancy. Similarly, seeds which were forced into dormancy may subsequently suffer induced dormancy.

(2) Immediate Germination Versus Innate Dormancy

Generally, evolution has led to the imposition of regulating mechanisms on seed germination which prevent the entire reproductive capacity of a species from being used up at once. Immediate germination is particularly disadvantageous to opportunistic species. Thus it might be expected that these three species would all have a high proportion of seeds with innate dormancy. Surprisingly, this is not the case.

Under optimum conditions, Steinbauer and Grigsby (1958) obtained 91% germination for freshly harvested *R. acetosella* seed, whilst *R. crispus* and *R. obtusifolius* gave almost complete germination (Steinbauer and Grigsby 1960; Cavers and Harper 1964). These results indicate that a very

low proportion of seeds are innately dormant. However, in nature, most seeds exhibit delayed asynchronous germination.

The contradictory statements in the literature about the occurrence of innate dormancy in the three species can probably be accounted for by differences in the germination behaviour of seeds from different localities and plants, and differences amongst the seeds of one plant. For example, Cavers and Harper (1964) reported that at 20°C in the dark, the seeds of one plant gave more than 50% germination whereas the seeds of eight other plants from the same area gave less than 3% germination. The shortcomings of using bulk samples have been pointed out by Salisbury (1965) and Cavers and Harper (1966).

Harper (1957A) stated that dry storage is required by *R. obtusifolius* seeds before germination will take place. Steinbauer and Grigsby thought that after-ripening is required for *Rumex* seeds. This anomaly is explained by the decreasing stringency of the requirements for germination in ageing seed. For example, Steinbauer and Grigsby (1960) found that *R. acetosella* seed at 20°C with light gave 29% germination when fresh, and 42% under similar conditions two years later. They obtained similar results for *R. crispus* and *R. obtusifolius*. The fresh seed of both species did not germinate at all without light and alternating temperatures. After two years, 57% of the *R. crispus* and 100% of the *R. obtusifolius* seed germinated under similar conditions. Furthermore, the germination rate of older seed is higher.

In an experiment in which fresh seed was tested for

innate dormancy, the percentage of seeds which germinated indicated that about 46% of *R. acetosella* seeds are innately dormant, compared to a maximum of 5% in *R. crispus* and none in *R. obtusifolius*.

(3) Induced Dormancy

(a) Introduction: Considerations of weed strategy predict that neither the seeds with induced dormancy, nor those with innate dormancy should all germinate as soon as suitable environmental conditions have been met (Harper 1967). This would result in the total loss of the seed reserve at one time should the plants suffer an environmental crisis before seeding. The intermittent germination which is predicted for the seeds of weedy species is observed in *R. crispus* and *R. obtusifolius* in the field. 'Maritime' *R. crispus* which is not weedy and is restricted to sea shore habitats does not exhibit strong dormancy (Lousley 1944).

(b) Dormancy inducing mechanisms: The mechanisms by which dormancy is induced in the seeds of these three species is not understood. Wesson and Wareing (1967) have proposed that as the seeds of many species require light for germination when taken from soil samples (but not in fresh samples), burial alters the seed response to light. Their inclusion of *R. crispus* amongst the seeds of species which undergo such an alteration in germination behaviour is questionable as Steinbauer and Grigsby (1960) have reported that fresh *R. crispus* seed gives zero or very low germination percentages in the dark.

(c) Differences in the potential for dormancy induction between seeds: The means whereby the seeds from one plant exhibit different germination requirements or require different stimuli to induce dormancy need to be explained. The differences in the germination behaviour from one plant may be due to genetic differences between seeds or to the environment of the seed during its development or dormancy. There are no reports that there is any genetic polymorphism associated with the differing dormancy behaviour of seeds from single plants in either *R. crispus* or *R. obtusifolius*.

Cavers and Harper (1966) have investigated the germination requirements of seeds from the same plants for different panicles, upper and lower halves of the same panicle and proximal and distal portions of the same panicle. I have observed that the numbers of seeds per whorl and the time of development of seeds are different on the main and secondary branches of panicles. This is particularly noticeable on the lower secondary branches which often tend to develop after the seeds on the main panicle mature. Furthermore, the seeds borne on the main and secondary branches differ in their access to the main vascular bundle and possibly in their food supply.

In a trial in which at least some seeds germinate, there may be a variety of reasons why the remainder do not. The seeds may be non-functional either because they are genetically faulty or because they have not completed their normal development. The conditions of the experiment may not provide the necessary germination stimulus for some of the seeds or may induce dormancy in others. Where the last

two cases apply there must either be a genetic or environmental difference between seeds on the same plant.

In their investigation of the germination polymorphisms of *R. crispus* and *R. obtusifolius* seeds, Cavers and Harper (1966) concluded: There are some differences in germination requirements between seeds from different panicles on the same plant, but that generally these differences are smaller than those between plants. However, some of these differences may be due to age differences between panicles. They found germination performance was not related to seed weight. In a comparison of seeds on the upper and lower halves of the panicle, no differences were observed except when germination took place in darkness. In this case the upper half of the panicle gave significantly higher germination percentages. The seeds of the upper half were significantly heavier than those of the lower half and had less specialized germination requirements. When seeds from the proximal and distal ends of the panicles were compared, the proximal ends were found to be heavier ($P < 0.01$) and had higher dormancy percentages when germinated in the dark but equally low dormancy percentages in the light. Cavers and Harper did not differentiate between tests which detected seeds with innate dormancy and those in which the experiment induced dormancy.

For the seeds borne on both the main and secondary branches of *R. obtusifolius* plants, the germination was so nearly complete that it is unlikely any of the seeds were innately dormant. It is probable that the slightly larger numbers of seeds from both the main and secondary branches

of *R. crispus* plants which did not germinate in the high temperature experiment were innately dormant. In the second experiment in which a lower temperature was used, the same proportion of seeds should have been innately dormant as in the first experiment. In addition to these, a further 11% of the seeds borne on secondary branches and 18% of those on the main branches did not germinate. This strongly suggests that the lower temperature induced dormancy in some of the seeds borne on the secondary and main branches, and to different extents. The different developmental environments of the seeds borne on the main and secondary branches accounts for some of the differences in their dormancy behaviour.

The simple hypothesis that these differences may be accounted for by differences in the nutrition of the seeds from the two environments is not supported if the final weight of a seed is indicative of its nutritional status. The weights of seeds borne on the main and secondary branches were not significantly different. A re-analysis of Maun and Cavers (1971) results for *R. crispus* also give the same mean weight for seeds borne on the main and secondary branches.

My results for *R. crispus* indicate that this difference in the developmental environments of the seeds borne on the main and secondary branches accounts for some of the differences in their response to dormancy inducing factors. However, even within seeds borne on primary or secondary branches there is a difference in their response to these factors.

This experiment only demonstrated the differential induction of dormancy in some seeds. It can probably be concluded that differential dormancy is generally induced by differences in microsite and to different extents in different seeds. The difference between the seeds is partially accounted for by their position on the panicle and the time at which they reached maturity.

In conclusion, a few seeds fall from the plant, encounter favourable conditions, and germinate. The majority undergo some kind of dormancy. In *R. acetosella*, and to a lesser extent in *R. crispus*, innate dormancy accounts for a proportion of the seeds which do not germinate immediately. The type of dormancy the rest of the seeds suffer is determined by the microsite into which they fall. Some of these sites have conditions which induce dormancy in a proportion of the seeds which fall into them. The rest present conditions unsuitable for germination, thereby enforcing dormancy on the remainder of the seeds.

(d) The release of seeds from induced dormancy: The release of seeds from induced dormancy must be affected by a relaxation of their germination requirements, a change in their position exposing them to different conditions or a change in climatic conditions.

As seeds of the three species become older their germination requirements become less specific, and when they do germinate their germination rates are greater. Periodic exposure to light, higher temperatures or alternating temperatures stimulate seed germination in all three species. The function of these triggers for seed

germination is clear if the possible fates of seeds falling on to the soil surface are considered in relation to the weedy strategies of these three species. As inhabitants of arable land and periodically cultivated or disturbed areas, many of the seeds are buried. After burial, reliance on environmental signals which indicate that the seeds have been returned to the surface will result in the greatest establishment rates. Roberts (1970) believed there was evidence that innate dormancy was most effectively overcome at the soil surface. The release of seeds from dormancy below a critical depth only results in their death, as their reserves are exhausted before they reach the surface. Light, and to a lesser extent alternating temperatures, are clear indications that the seed is at a depth from which its resources will allow it to emerge. The seeds of all three species give far greater germination percentages in the light than in the dark. If light is present, the requirement for alternating temperatures is reduced.

In the absence of light, alternating temperatures will promote germination in many of the seeds. For example, Steinbauer and Grigsby (1960) found that *R. obtusifolius* seeds in the dark and at a temperature of either 20 or 30^{o}C did not germinate. However, 18% germinated when the temperature alternated between 20 and 30^{o}C. In soil, temperature alternation takes place only in the top few centimetres, the temperatures of deeper soil remaining relatively constant.

The decreasing stringency of the germination inducing requirements in ageing seed may result from the following

strategy: As the maximum survival time for buried seed approaches, germination under any conditions must give a higher establishment rate than no germination at all. However low the percentage of seeds which become established in this way, it must be greater than that resulting from the situation in which seeds maintain the stringency of their germination requirements. Such seeds would not be induced to germinate at all. In the same experiment outlined above, Steinbauer and Grigsby (1960) found that two year old *R. obtusifolius* seed in the dark, and with alternating temperatures germinated completely.

Although two year old *R. crispus* and *R. obtusifolius* seeds gave equal or higher germination percentages than fresh seeds under all conditions, the behaviour of two year old *R. acetosella* seed was different. In most cases, older *R. acetosella* seed gave lower germintion percentages than fresh seed. This is probably due to the shorter seed longevity of this species rather than the adoption of a different germination strategy.

(4) Enforced Dormancy

(a) Introduction: Enforced dormancy is a tactic which can be selected for only in that the seeds must be physiologically able to survive the periods over which dormancy is likely to be enforced. The period for which *R. acetosella* seed is viable in soil is relatively short. Both *R. crispus* and *R. obtusifolius* can survive for extended periods in the soil as documented below.

(b) Mechanisms by which dormancy is enforced: Seeds are forced into dormancy when conditions which are

unsuitable for germination prevail, e.g. following burial. Harper (1957A) suggested that high CO_2 and low O_2 tension may be responsible for enforcing dormancy on buried seed. To support this theory he referred to unpublished work by Chancellor in which seed buried under a variety of plant communities failed to emerge, but emerged readily when the soil was disturbed or the seeds were planted in arable soil. However, that "carbon dioxide narcosis" is principally responsible for enforcing dormancy is disputed by Wesson and Wareing (1967). They believe that the absence of light is the principal factor preventing germination of buried seed. Contrary to expectation, germination of seeds on the soil surface may also be prevented by a lack of light. Taylorson and Borthwick (1969) demonstrated that the germination of *R. obtusifolius* is inhibited by leaf filtered light almost to the level of dark controls.

Kolk (1962) came to similar conclusions about *R. crispus* when he found that light, and to a lesser extent alternating temperatures, broke seed dormancy. He found no evidence of inhibitory substances, or significance in oxygen levels.

(5) Seed Longevity and Mortality

Seeds which do not encounter the conditions required to release them from innate or induced dormancy or which suffer enforced dormancy for too long, die. Roberts (1970) related the breakdown process to intrinsic changes in the embryo which depend on time, temperature and moisture levels. Kolk (1962) attributed the durability of *R. crispus* seeds to the embedding of the embryo in the perisperm and the three

layer pericarp. However, his conclusion that the deterioration of the highly cuticularized and suberinized seed coat is an almost essential adjunct to germination, cannot be correct. This is shown by the ability of many *R. crispus* seeds to germinate immediately.

The longevity of *R. acetosella* seed in the soil is not known. A calculation based on the percentage germination of one, two and six year old dry stored seed (Steinbauer and Grigsby 1958) suggests that nearly all seeds would have lost their viability after 20 years. Soil stored seeds are unlikely to retain their viability for much longer than air stored seeds.

Darlington and Steinbauer (1961) carried out the 80 year test on Dr Beale's seed viability experiment. As only 2% of the *R. crispus* seeds germinated, they concluded that its period of viability was almost finished. This was confirmed by Kivalaan and Bandurski (1973) who found no viable *R. crispus* seeds in the 90 year test. Fifty-two per cent of seeds were viable after 50 years in the same experiment. The longevity of *R. obtusifolius* seeds has not been tested for such extended periods, but in Durvel's buried seed experiment seeds germinated after 40 years (Toole 1946).

Seed mortality may be the result of intrinsic changes in the embryo, as explained above, or damage to the seed by predation, soil micro-organisms or soil dwelling animals.

(6) Conclusion

The classic viewpoint that dormant seed is one of the

safest forms in which a plant can exist is true insofar as in this form it is insulated from ecological succession and natural selection. However, pre-emergence mortality may be very high. Sagar (1970) suggested that the greatest significance should be attached to pre-emergence mortality. The disadvantages of soil seed mortality and the sacrifice of some of the potential fitness (Harper and White 1974) must be greatly outweighed by the advantage of asynchronous germination and temporal seed dispersal in the weed strategy.

CHAPTER VII

THE ECONOMIC SIGNIFICANCE AND CONTROL OF DOCKS AND SORRELS

I. INTRODUCTION

All three species are of economic importance. *R. acetosella* can be a food in grazed farmland or an aggressive weed in cropped areas or market gardens. Both *R. crispus* and *R. obtusifolius* are serious weeds of grassland, arable land and in market gardens. They compete directly with crops for environmental resources, lower the quality of hay and seed crops with seed contamination, and may exhibit allelopathy towards other plants (Einhellig and Rasmussen 1972).

The principal factor in the success of *R. acetosella* as a weed is probably its mode of vegetative reproduction which allows it to compete with other species and extend its range in conditions unfavourable to the establishment of seedlings. *R. crispus* and *R. obtusifolius* probably succeed as weeds not only because of their competitive ability but also by the production of a large number of seeds with varying dormancy mechanisms.

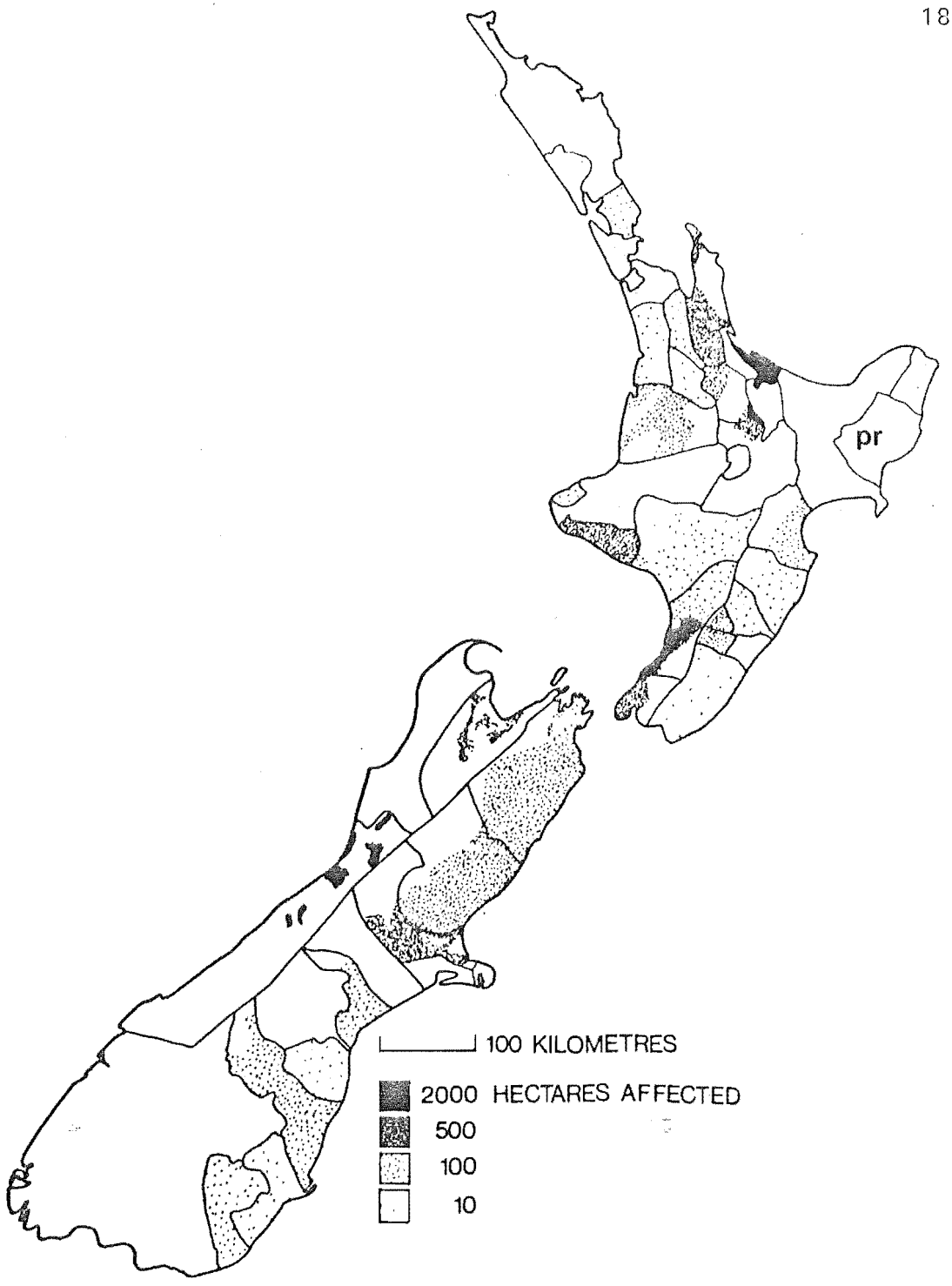
(1) The Distribution and Severity of The Dock and Sorrel Problem

R. acetosella, *R. crispus* and *R. obtusifolius* are all serious weeds on a variety of classes of agricultural land.

Lousley (1944) referred to *R. crispus* as a "rampant pest", whilst Putwain (1970) described *R. acetosella* as a widespread, versatile and troublesome weed. All three species are of worldwide distribution.

R. acetosella was principally a sand dune inhabitant but is now more frequent on agricultural land (Harper 1957B) where it prefers sandy soils and disturbed habitats. *R. crispus* and *R. obtusifolius* present a control problem on some area of nearly all farms (Evans 1968). They are a particular nuisance on land which is inherently wet or where rainfall is high. In such areas, the high water levels lead to treading and poaching of the sward which produces bare areas conducive to dock establishment (Evans 1968).

A relative measure of the severity of the dock and sorrel problem can be made using the regulations governing their status as noxious weeds and the presence of their seed in seed crops in various countries. In Britain, all species of docks and sorrels were listed under the Seeds Act 1959 as injurious weeds, and their presence in cereal, grass, clover and field seeds had to be declared by the seller. In cereals, the presence of one dock or sorrel seed found in a prescribed sample had to be declared, whilst for grasses, clovers and field seeds, the number of seeds in excess of one in a sample had to be stated (Anon 1962). However, these regulations were ineffective in reducing the frequency of occurrence of *Rumex* spp. in samples of herbage seed between 1922 and 1951. *R. crispus* frequently infects crops, being the most frequently found weed seed in small seeded grasses, the second most frequent in clover and lucerne, fourth in cereal seeds and fifth in grass seeds (Wellington 1960).



Map 2. The severity of the dock problem in New Zealand. Stippling density shows the number of hectares affected within the area open to dock infection in each statistical region. No data was available for six regions. Docks were only recorded as present (pr) in one region.

From May and Baker and Department of Agriculture survey.

R. crispus is also commonly found in the seeds of oats, wheat, barley and red clover. *R. acetosella* seed is found in the seeds of Italian rye grass, perennial rye grass, timothy, cocksfoot, crested dogs tail and white clover (Anon 1962). The British Ministry of Agriculture can compel an occupier of land to destroy *R. crispus* and *R. obtusifolius* plants within a specified time under the Weeds Act 1959. E.E.C. regulations require that the number of *R. crispus* and *R. obtusifolius* seeds shall not exceed 2 in a sample of 5 g. In Western Australia, *Rumex* spp. are a prohibited species in seed crops. In the United States, all three species are included in the noxious weeds of several states, where their seeds are frequent contaminants in forage crops such as clover and grass seed and agricultural seeds, particularly small seeded legumes, millet and seeds of similar size (Steinbauer and Grigsby 1960). In New Zealand, none of the three species are classed as noxious weeds under the Noxious Weeds Act 1950, nor are there any regulations governing the amount of *Rumex* seeds in seed crops.

In 1968 the severity of the dock problem in New Zealand was assessed in a survey carried out by May and Baker and the Department of Agriculture. The survey was based on a questionnaire sent to Department of Agriculture farm advisory officers. It classifies approximately 46,500 acres of pasture and 3,000 acres of lucerne as being infested with docks to a degree that would make chemical control economical (Map 2).

The comments of the farm advisory officers participating in the survey indicated that the dock problem is increasing in New Zealand, especially in areas of high

fertility or where fertility is increasing and areas where winter pugging is common. Dairy farms are the most severely affected.

The severity of the problem is also increasing in lucerne and red clover crops. The lack of regulations governing the presence of *Rumex* seeds in red clover seed may account for the increasing problems in this seed crop.

There are no figures available on the frequency with which *Rumex* spp. contaminate seed crops in this country (S. Clark, Palmerston North Seed Testing Station - pers. comm.). However, *R. acetosella* is a frequent impurity in white clover and ryegrass crops and also occurs with medium frequency in all small seeded agricultural crops; for example, red clover, cocksfoot, brassica, browntop and lucerne. *R. crispus* and *R. obtusifolius* (collectively included under *Rumex* spp. because of the difficulty of accurate seed identification) are frequent impurities in red clover and lucerne and occur with medium frequency in all other small seeded crops as for *R. acetosella*.

(2) The Competitive Ability and Damage Inflicted on Crops by Docks and Sorrels

(a) The competitive ability of docks and sorrels: The benefits of a weed control programme depend on the damage the desired plants suffer from competition with the weed, the level of weed infestation and the efficiency and side effects of the control method. The costs of controlling the weed must be measured in terms of the materials and labour used and losses in production due to the herbicide, as well as any long term dangers of the herbicide.

The importance of the weed in question should really be known before control measures are instigated. Both its ranking amongst other weeds (Sagar 1968) and its competitive ability should be known. There is, however, little knowledge on the competitive ability of weeds (Chancellor 1968), most attempts to define and measure it having failed (Sagar 1968). In a study carried out in England by Savoury and Soper (1970), docks accounted for 100% of the cover in one of their control plots, whilst Courtney (1970) in N. Ireland found that the contribution of docks to the total herbage was 54%. Although precise figures are not available, Courtney (1970) asserts that grass yield was increased when docks were controlled. Sagar (1968) points out that even if weeds are not competing with the crop, the dry matter the weed has gained represents a failure on the part of the crop to exploit the environment to the fullest extent. Some of the economic or production losses can be measured more directly, for example, the decrease in yield or reduction in quality of crop seed by its infection with dock seed or the reduction in fodder quality (Courtney 1970).

There are no accurate figures available for the competitive ability of docks growing under New Zealand conditions. However, estimates made by the farm advisory officer for the Piako district in the combined May and Baker and Department of Agriculture report placed production losses in problem paddocks as high as 30%. Estimated dry matter losses of 15% were reported for the Waikato area and 20% for the Palmerston North area. Estimated production losses were as low as 5% for some other areas.

The effectiveness of a herbicidal control programme

is related to the initial level of dock infestation. The efficiency of a control method should be assessed primarily in terms of the increased yield of the desired species, although other benefits of controlling docks must be considered. These include the improvement in the quality of hay, fodder and seed crops and long-term benefits such as favourable alteration of the sward composition, and lower weed infestation levels in the future because of a decrease in the number of plants producing seed.

However complex the problem of accurately assessing the cost to benefit ratio of dock control, farmers, horticulturalists, orchardists and market gardeners frequently feel on an intuitive basis that it is necessary.

(b) Direct damage inflicted on crops and grassland by docks: The injury that dock plants do to crops is primarily through direct competition for moisture, soil nutrients, space and light (Meadly 1958). Competition for these resources leads to a decrease in the yield of a variety of crops. This is documented elsewhere. It is also possible that allelopathic effects contribute to the damage that these species do. The data of Einhellig and Rasmussen (1972) clearly indicate that aqueous extracts from *R. crispus* are strongly inhibitory to grain sorghum *(Amaranthus retroflexus)* and field corn. They suggest that the leaching out of water soluble phenol ics from *R. crispus* plants accounted for the inhibitory effect of these plants on the growth of other species. Field sampling showed a reduced biomass in quadrats near *R. crispus* plants as well as poorer establishment of several species. Their data suggested that

allelopathy may be important in the early invasion of waste areas by *R. crispus*. As *R. obtusifolius* also exhibits similar successional behaviour it too may have allelopathic effects on other species. *R. crispus* has been recorded as harbouring the crowngall pathogen, *Pseudomona tumefaciens* Sm. and Town., (Muncie 1930). As the hosts of this pathogen are principally plants of economic importance, it is possible that *R. crispus* may carry the disease from year to year in fields planted in non-susceptible crops.

The quality of crops is reduced by the presence of dock plants in a variety of ways. Lescar (1970) states that they make fodder production difficult and decrease the quality of hays. Lucerne may have to be harvested at an earlier date to prevent docks from seeding. Docks hinder the drying of crops prior to bailing for hay and can cause deterioration in bailed lucerne. The contamination of cereal crops and seed crops with dock seed is deleterious. Economic losses are incurred cleaning seed and through its decreased value, particularly in seed for export (e.g. red clover seed). Furthermore, future infestations of dock plants will be increased.

Although stock do not generally feed on docks unless pastures are overstocked (with the exception of sheep which often eat the younger leaves out of the crown), accidental ingestion of docks does occur. Meadly (1958) reports gastric disturbances and dermatitis in stock which consumed docks. Cavers and Harper (1964) cite Pamell (1911) who claimed that consumption of *R. crispus* induces nausea, copious urination, watery brown faeces, a dry spasmodic cough and perspiration in farm animals. Docks have also been reported

as increasing the possibility of facial eczema (May and Baker and Department of Agriculture report). Poultry may also be harmed by consuming docks.

II. THE EFFECT OF CULTIVATION ON EXISTING AND FUTURE POPULATIONS OF DOCK SOIL SEEDS AND PLANTS

Cultivation may serve many different functions which are not related to weed control, such as the ploughing in of manure, soil loosening, aeration, the removal of the remains of old crops, seed bed preparation etc. However, Harper (1957A) believes that weed control is the main consideration in the planning of soil cultivation. Here, cultivation may serve to stimulate the germination of seeds buried in the soil, to bury seed from mature plants below the depth from which it can emerge and to break up and destroy mature weed plants.

The use of mechanical cultivation for the control of dock plants has been advocated frequently; e.g. Cavers and Harper (1964) who stated that a series of rotary cultivations may be useful in controlling *R. obtusifolius* and that cultivation can easily destroy the seedlings, Meadly (1958) who believed that good results were obtained by systematic cultural and chemical treatments, and an anonymous (1962) Ministry of Agriculture, Fisheries and Food Advisory leaflet which stated that ploughing was necessary to eradicate docks from a seriously infected field. However, some of the literature dealing with cultivation as a method of weed control does not fully examine the effects that cultivation has on the different age classes of dock

seeds and plants. Cultivation which is not fully coordinated with the life cycle of the weed and any crops which are to be grown, and systematically related to chemical control methods, could increase the buried soil seed, the competition between the weed and crop, the standing weed plants or the total seed set by the weed. For example, Cavers and Harper (1964) stated "Cultivation facilitates the germination of new seeds, as seedlings tend to appear mostly on open ground, cultivated land or pasture where the turf has been destroyed."

(1) Commonly used Cultivation Techniques

Cussans (1966) has categorised the techniques by which land may be prepared for the sowing of crops and their influence on weed growth into three types: (a) Ploughing and subsequent cultivation. This buries surface vegetation and weed seeds, inverts the soil so that previously buried seed is brought to the surface and disturbs the soil, breaking up rhizome systems and roots whilst providing suitable conditions for weed seed germination. (b) Cultivation without ploughing. Here the disadvantages of ploughing are present but to a much smaller extent. Using this method the amount of seed buried is low. (c) Direct drilling. Theoretically the soil is disturbed least by this technique although implement wheels etc. will disturb the soil to a certain extent. Here the effect of these cultivation techniques (and the need to cultivate) on existing and future populations of docks and sorrels are discussed. The effects on the buried and surface seed population, seedlings and mature plants are

discussed in turn.

(2) The Effects of Cultivation on the Buried Weed Seed Population, Particularly of *R. crispus* and *R. obtusifolius*

The effects of cultivation on buried weed seeds will depend on the method of cultivation (techniques which will alter the depths of soils and thus weed seeds, or break large clods into fine soil having the greatest effect), the type of dormancy regime the seeds are under and the means by which it may be broken, and the persistence of the seeds in soil.

Roberts (1963) states that any consideration of the long-term implications of modern weed control techniques must take into account the population of dormant viable seed present in the soil. *Rumex* spp. produce large numbers of seeds which may remain viable in the soil for extended periods of time. Cavers and Harper (1964) quote Duvel's buried seed experiment in which *R. obtusifolius* seeds germinated after burial for 40 years in the soil at depths of about 50 centimeters and 100 centimeters, and after 30 years at depths of about 20 centimeters. Lewis (1973) also found 30% seed viability after burial for 20 years at a depth of 13 centimeters. The length of time for which *R. acetosella* seeds may remain viable in the soil is not known. It is possible that they are able to survive for periods of up to 20 years.

(a) How cultivation may stimulate weed seed germination: Wesson and Wareing (1967) have studied the seeds of many species including *R. crispus*, and concluded

that a light requirement is the chief factor controlling the dormancy of buried seed. Thus cultivation which brings viable, buried weed seeds to the surface where they can be released from their requirement for light will encourage the germination of a proportion of the seed which was held under conditions of induced dormancy. They also believe that soil burial induces dormancy by altering the germination requirements of seed from species initially unaffected or inhibited by light.

Cultivation which does little to disturb the various soil layers may also encourage the germination of weed seeds near the surface. Taylorson and Borthwick (1969) have discovered that germination is inhibited by leaf filtered light almost to the level of dark controls. Thus methods of cultivation which only remove some of the ground cover may encourage the germination of weed seeds by changing the predominant wave length of light incident on the seeds.

The removal of existing vegetation by cultivation or other means may also release seeds from dormancy by other processes. For example, Harper (1957A) believed that actively growing vegetation may be a factor in enforcing dormancy, and referred to the emergence of large numbers of *Ranunculus* spp. after plots covered in grasses were bared by spraying with dalapon (2:2-dichlor-propionic acid). Furthermore, the destruction of vegetation may change the soil atmosphere by killing the plant roots which previously maintained a high CO_2 and low O_2 tension. High soil atmosphere tensions of CO_2 and low O_2 tensions have been shown to enforce dormancy on buried seeds (Harper 1957A) or induce dormancy in seeds. A similar effect may be achieved

by cultivation which breaks up the soil and aerates it. The reverse effect on soil O_2 and CO_2 tensions takes place when the remains of crops, such as hay stubble, are ploughed in. The decay of the buried vegetation will increase the soil CO_2 tension and lower the O_2 tension, and possibly induce or enforce dormancy on the seeds buried during the ploughing.

The preparation of seed beds by cultivation and rolling, or the use of seed drills with press wheels results in the germination of a higher proportion of the buried weed seed than might be expected. The resultant "flush" of weed seedlings experience ideal conditions for establishment, and compete strongly with the young and vulnerable crop or vegetable seedlings.

(b) Cultivation to reduce the buried weed seed population: Because it stimulates the germination of weed seeds, cultivation has been considered as a means of reducing the buried seed population. The germination of seeds which have their dormancy broken at a level from which they are unable to emerge will decrease the buried weed seed population, as will the germination of seeds near the surface. The decline in the number of buried seeds follows an exponential pattern (Roberts 1970). Without soil disturbance, the buried weed seed population decreases by about 20% per year. Cultivation twice a year to a depth of 23 centimeters will decrease the soil seed population by 42% per year, and with seven cultivations, by 56%. Reinfection from nearby seed sources such as hedgerows or as a contaminant of crop seed must be avoided.

Cultivation as a means of reducing the buried seed population is not practical, because of the diminishing returns resulting from each cultivation and the high number of cultivations needed to achieve effective results. Roberts (1970) concludes that cultivation solely to reduce the buried seed population has no virtue, because each cultivation affects such a small proportion of the seed, probably less than five to ten per cent. Cultivation is only advisable if it serves some purpose other than weed control and an effective method of controlling weed seedlings is available.

(c) The effects of different degrees of cultivation: Bleasdale and Roberts (1960) have shown that as tilth fineness increases, so does the number of weeds which emerge. Harrowing which produces a clod size of 1-5 centimeters results in a 60% lower seed emergence than fine harrowed tilth, broken up to clods of less than one centimeter in diameter. Rolling results in a similar increase of 60%. The use of a press wheel with a crop sowing drill on medium - fine seed beds increases weed emergence by 12%, and on coarse seed beds by 36%.

The use of non-cultivation or minimum cultivation techniques will minimize weed seed germination by imposing permanent dormancy on 90% of the seeds, e.g. in fruit culture (Roberts 1970). The number of viable seeds will decrease from year to year. This method of restricting the germination of the buried weed seed population is not an effective control measure for *R. acetosella*, which is also able to propagate vegetatively. Non-cultivation is also a soil conservation measure.

(d) Minimum cultivation: If cultivation is essential for reasons other than weed control; for example, seed bed preparation, it should be minimized and restricted in depth, so that enforced dormancy is maintained on the deeper seeds and the return of seeds to the surface from shallower levels is minimized. Bleasdale and Roberts (1960) conclude that if cultural methods are to be used for weed control it is advisable to use the roughest seed bed compatible with securing good crop establishment, as this will result in the survival of fewest weeds. However, if herbicides can give almost complete control, they advocate the use of a fine seed bed as this will lead to the greatest depletion of soil seed reserves. Harper (1957A) also argues that for permanent weed control, ploughing should be avoided and surface tillage reduced to a minimum. Weed seedlings should be killed with herbicides when they emerge. Buried weed seeds can then be ignored as they are unable to return to the surface.

The use of direct drilling is the best solution to the problem of preparing a fine seed bed without stimulating the germination of weed seeds. If specific and effective herbicides are available (as they are for *Rumex* spp.) they should be used in combination with direct drilling to control weed seeds which do emerge. The closer the application of the herbicide to the time of drilling, the more weed seedling development and regrowth will be retarded. Allowance must be made for the effects of residual herbicide on crop growth (Cussans 1966).

(3) The Effect of Cultivation on Seedlings

Seedlings in previously cultivated land can be controlled easily by cultivation during the early stages of their development. At later stages, cultivation will only kill a proportion of the plants, the remainder being able to re-root and grow if they are intact. However, the removal of seedlings in this way encourages the germination of dormant seeds and leaves them without any competition, conditions which are particularly favourable to the establishment of dock plants. In arable land, cultivation is not a practical way of controlling seedlings, and will encourage the germination of dormant seeds. The destruction of seedlings in establishing crops is also not practical, because of the ensuing damage to crop seedlings. Thus the removal of weed seedlings from vegetables, crops or arable land is either inadvisable or impractical. Herbicides are the most effective way of controlling seedlings.

(4) The Effect of Cultivation on Mature Dock and Sorrel Plants

Mature *R. acetosella* plants are unable to survive thorough burial (Anon 1962) although they are able to survive being cultivated once or twice. The application of lime will often control sorrel effectively (Anon 1962).

The efficiency of ploughing and other cultivation techniques for the control of dock plants is a controversial subject. Some of the controversy revolves around the ability of dock plants to regenerate from root fragments.

Soil cultivation in the presence of mature plants will affect whole plant regrowth, the regeneration of plants

from root fragments and the burial of seeds. Methods of cultivation which merely disturb the soil or turn it without pulverising it, e.g. ploughing, will not eradicate dock plants. The plants will be either dislodged or turned upside down and will recover rapidly, even if the roots are left exposed to the sun. I have observed dock plants in a recently disced field which were upside down with the leaves buried and the roots exposed. These plants were able to recover rapidly, the new leaves growing up between the roots. Fine cultivation which chops up the plant or severs the root from the stem is said to hinder clearance, as many parts of the split crown will grow, especially in *R. obtusifolius* (Anon 1962). My own observations have confirmed that larger portions of the crown do regenerate, although the number of "new" plants does not reach the previous "effective" plant number in that season.

Meadly (1958) stated that a number of cultivations are usually necessary to prevent the cut portions of root resulting from cultivation from developing into new, independent plants. Cavers and Harper (1964), referring to *R. obtusifolius* made a similar statement about root regeneration. They outlined the controversy about the ability of *R. crispus* to regenerate from root fragments, and concluded that generally only the top few centimeters of the tap root were able to produce new plants, except in portions detached in the early spring. Hudson (1955) obtained similar results and found that there is a high degree of seasonal control over the ability of *R. crispus* to regenerate from root fragments. He observed almost no regenerative capacity in the roots of *R. obtusifolius*,

although small portions of the true root regenerated in springtime. He concluded that dock root cuttings do not appear to regenerate freely at any time of the year although roots severed and left undisturbed *in situ* regenerate strongly.

In an experiment carried out to test roots for their ability to regenerate, no portion of the root could be induced to produce shoots. The disagreement in the literature about the ability of root fragments to regenerate is perhaps due to confusion between the root and the contractile shoot. The contractile shoot may bear dormant buds which will develop readily if the other buds are damaged, as explained previously.

The regeneration of plants from root cuttings is not a serious problem after cultivation has been carried out. The only shoots which were produced were on the top portion of the roots and were probably from pre-existing buds. The total number of plants is not increased greatly, if at all after such treatment. The final yield of plant mass or seed set is severely reduced by such cultivation.

Mowing to remove reproductive panicles before seed is set is not entirely effective. Cavers and Harper (1964) stated that mowing is often advantageous to established *R. obtusifolius* plants. New shoots are sent up and autumn flowers can be produced very quickly.

To assess the practicability and effectiveness of mowing dock plants after flowering to reduce seed set, an experiment measuring the viability of *R. crispus* and *R. obtusifolius* seeds cut at various stages of maturity was conducted. As some plants are able to mature their seed

after being cut, it is necessary to know how early the weed has to be cut before seed is unable to mature successfully. This is not only important to weeding operations but also to hay production, where dock seed may contaminate the hay.

With regard to weed control, the possibility that some seeds are capable of germination after mowing must be minimized. The experiment showed that *R. crispus* seeds are able to mature on panicles cut just after the green seed stage. *R. obtusifolius* seeds are able to mature if the panicles are cut just after the end of flowering.

The differences between the results presented here and those of Gill (1938), who had higher germination percentages for *R. crispus* seeds (88% for milk ripe seeds and 84% for dead ripe seeds), is probably accounted for by the different measures of seed maturity used in the two experiments.

More recently, Maun (1974A) conducted extensive experiments of a similar type on *R. crispus* plants. However, he measured seed maturity in days after anthesis and employed different post-cutting conditions which makes comparisons with the results presented here difficult. In the treatment most similar to the one used here, he obtained 15% germination from seed removal 12 days after anthesis. Thirty days after anthesis the same treatment gave a germination percentage of 54.

The higher germination percentage achieved by Maun was possibly due to the higher humidity experienced by the cut panicles, allowing their leaves to survive for a longer period and permitting manufactured food to be translocated

from them to the seeds. Although the germination percentages under field conditions would be lower than those obtained here because a proportion of the seeds would be dislodged from the panicle during mowing and thus not receive any nutrition from the panicle leaves, *R. obtusifolius* plants should be mown during flowering and *R. crispus* plants no later than when the seeds first start to swell.

Mowing once a season may significantly reduce the potential seed pool for that season. However, there are two possible complications. Not all of the seeds reach maturity at the same time, which may make it necessary to mow the area more than once. It is also likely that the plants will initiate the development of new panicles if the first panicles are removed before they reach maturity and the necessary resources are available (Cavers and Harper 1964).

Ploughing in of mature plants which are not bearing seeds will result in a lower "effective" number of dock plants and a reduced seed set for that season. However, the soil disturbance will release a large number of seeds from enforced dormancy the following season. Mowing may be most effective when used in conjunction with a selective herbicide. If the dock plants are mown when they are in flower in the late summer, seed set will be reduced and extensive regeneration and autumn flowering will be induced. Advantage can be taken of the regeneration about two months later, as it maximizes herbicide absorption.

In conclusion, a minimum of carefully controlled soil disturbance used in conjunction with a selective herbicide is the most effective way of preventing the germination of

large numbers of buried seed, reducing the number of seedlings and seed set and the total mass or "effective" number of reproductive plants.

III. CHEMICAL CONTROL OF DOCKS AND SORRELS

(1) Introduction and Early Herbicides

This section synthesises the knowledge on the control of docks by chemical means, considers this knowledge in relation to the ecology of the weed and New Zealand conditions, and suggests future directions that the control of these weeds might take. Amongst the troublesome weeds in the genus *Rumex*, *R. crispus* and *R. obtusifolius* are most important. The control methods outlined here also apply to *R. conglomeratus* which occasionally occurs in grazed land in New Zealand. *R. acetosella* is also mentioned as it sometimes presents a serious control problem.

Until recently, the principal chemicals used for dock control were M.C.P.A.,* 2.4-D, 2.4-D ester, M.C.P.B. and 2.4-D.B. (Cavers and Harper 1964). However, dock control with these chemicals is not satisfactory, regeneration from roots and large portions of the crown being frequent. More recently, Lescar (1970) has tried combinations of 2.4-D picloram and M.C.P.A. or 2.4-D and

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*M.C.P.A. 4-chloro-2-methylphenoxy acetic acid
2.4-D 2.4-dichlorophenoxyacetic acid
M.C.P.B. 4-(4-chloro-2-methylphenoxy)butyric acid
2.4-D.B. 4-(2.4-dichlorophenoxy)butyric acid
picloram 4-amino-3,5,6-trichloropicolinic acid
dicamba 3,6-dichloro-2-methoxybenzoic acid
mecoprop dl 2-(4-chloro-2-methylphenoxy)propionic acid(MCPP)
2,3,6-TBA 2,3,6-trichlorobenzoic acid

dicamba without good results and 2.4-D with picloram or 2.4-DP, 2.4-D and picloram with good results. Maun and Cavers (1969) have investigated the effect of 2.4-D on the seed production of *R. crispus*. They found that spraying with 2.4-D just before anthesis almost completely prevented fruit and seed production. None of the seeds which did develop following pre-anthesis spraying formed embryos. Of those sprayed at anthesis, only 2% formed rudimentary embryos. This method of control does not usually affect the plants, the buried soil seed or seed from unsprayed plants. Furthermore, the practical problems of spraying plants with varying times of anthesis at the correct time make it impractical to use in the field. However, spraying cereal crops with 2.4-D, M.C.P.A., M.C.P.B. 2.4-DO, mecoprop, M.C.P.A./dicamba and M.C.P.A./2,3,6-TBA destroys any seedling docks which have germinated, as well as preventing seeding (Anon 1962).

(2) The Control of Docks with Asulam (Asulox)

(a) The discovery of asulam: In 1961 a group of three ethyl benzenesulphonylcarbamates which had been prepared for evaluation against avian coccidiosis exhibited interesting effects on grasses normally resistant to foliage herbicides. These effects led to the development of three other compounds, one of which (M & B 9555 - CH_3OOCNH-C$_6$H$_4$-$SO_2NHCOOCH_3$ or 4 methoxycarbonylamino) has subsequently been named asulam (Ball, Cottrell and Heywood 1965). In its commercial form, Asulox, it is used specifically for the control of docks. Asulox is the aqueous concentrate formulation of asulam, containing 40% w/v asulam. Asulam

is selectively absorbed by the leaves of some species and translocated from there to the apical and axial meristems where it interferes with vital growing processes (Ball *et al.*). A slow systemic reaction takes place with susceptible plants becoming chlorotic and often bright yellow. After some weeks, during which no new growth takes place, the plants die. Some leaves or parts of leaves absorb asulam more readily. Absorption is rapid, exposure for one hour being as effective as exposure for 24. Seedlings fail to develop in dilute solutions of the chemical. The selectivity of plants for the chemical is not as high with root applications. Soil type has no effect on its action.

Because Asulox is the most effective means of controlling docks, and it is the most commonly used herbicide for docks, the remainder of this discussion relates to Asulox unless other herbicides are specifically mentioned.

(b) Asulox dosage: The effectiveness of treatment does not decrease as the dock infestation gets higher (Evans 1968).

The effectiveness of Asulox in controlling docks is proportional to the dosage at which it is applied. At higher doses of two and a quarter to three times the commercial rate (1.12 kg/ha) complete and lasting control of docks and *Holcus lanatus* was achieved by Ford and Combellack (1966). At this application rate *Agrostis stolonifera* was checked whilst *Lolium perenne* was resistant. Although it gives better residual activity when applied at this rate, Asulox favours pasture species at doses below

three to four times the commercial rate. Blair (1968) found that at doses of two times the commercial rate there was a decrease of only 50% in the number of dock plants after 32 weeks. However, his test was not carried out at a suitable time of year. If Asulox is applied in the correct season it gives good control at the commercial rate of application. The commercial application rate is the best compromise that can be achieved for grassland between efficiency, cost of application and damaging side effects.

(c) Timing of Asulox application: The developmental stage of the docks at which application is made is critical. Courtney (1970) found Asulox gave poor control when it was applied at the incorrect stage. The timing of application depends on two factors: the times of year at which docks are most susceptible to herbicides, and the times of year at which a slight drop in crop or sward yield is deleterious. Courtney (1970) stated that the optimum stage is between the release of the first leaf and the production of the first node on the reproductive panicle, the length of the period depending on the developmental speed of the docks as well as climatic factors. Miles and Isaacs (1969) carried out tests in New Zealand and found that the commercial rate of application gave 80% control in spring and 58% control when applied in autumn. The autumn application took longer to act. At one and a half times the commercial rate, spring and autumn application gave 99 and 82% control respectively. The reduction in cover frequently exceeded these figures. The tests carried out in autumn caused greater damage to pastures which did not recover until the following spring.

However, for lucerne, application should be made during the autumn once the dock have recovered from the last cut. Lucerne is susceptible to Asulox at some stages of its growth (Ball *et al.* 1965).

There are some circumstances in which it is more important to avoid the slight setback experienced by the crop or sward than using the herbicide at its most effective time. For example, under intensive management schemes, such as rotational or strip grazing, even a small loss may be significant (Soper 1970). Here the reduction in yield of the spring growth can have an adverse economic effect on an intensively stocked farm. In these circumstances there is a dependence on the spring "flush" of grass for grazing and silage or hay for winter feeding. Under such circumstances, Martin (1970) suggests that the use of Asulox at the end of summer should be considered even though it is less effective at controlling docks at this time of year. Evans (1968) proposed that spraying in autumn at a higher dosage followed by spring spraying where necessary at a lower dosage may avoid the decrease in production at the peak of the season.

Asulox is primarily absorbed by dock plants through actively growing and undamaged leaves. As the vigour of dock plants and the entirety of their leaves is decreased by mowing, grazing or trampling, an interval of a few weeks should be left between grazing or mowing and Asulox application.

(d) The time Asulox takes to act: Asulox acts very slowly. Savoury and Soper (1970) found that the best

results were not achieved until two to four months after spraying, whilst Ford and Combellack (1966) found that seven months were needed for the optimum effect. Miles and Isaacs (1969) found that the rate of action could be improved by the addition of 2.4-DB, but not the final result.

The amount of damage that Asulox application does to pastures or crops is dependent on the dosage at which it is applied, the proportion of susceptible species, the vigour of the pasture or the time of year at which application is made, and the interval since it was last cut or grazed. The damage done to susceptible crop and pasture species is directly proportional to the dosage rate. As dosage is increased the yield of desirable species decreases making accurate application essential. Martin (1970) measured a dry matter decrease of one half after spraying at four times the commercial rate. At the commercial application rate the damage to desired species is minimized without reducing the effectiveness of the herbicide below acceptable limits. However, five months after spraying Asulox at three times the commercial rate, Ford and Combellack (1966) found that although *Poa* spp. had been severely damaged they recolonized quickly from seed and also moved into the bare patches left by dying docks. After seven months, desired species had increased. When Asulox was applied at the commercial rate, Soper (1970) found no decrease in the dry matter yield of rye grass, whilst Martin (1970) found that pasture recovered within six weeks of spraying.

(e) Side effects of Asulox application: As the proportion of susceptible species in the sward or crop

increase, the damage caused by Asulox will increase. For example, the damage to pastures containing a large proportion of *Holcus lanatus* is severe. However, its susceptibility ultimately results in improved pastures as it is replaced by more desirable species.

The more vigorous the desired species are, the more quickly they will recover from damage and move into the bare areas left by dying dock plants. For this reason immature pastures are more susceptible than mature ones. Miles and Isaacs (1969) found that immature pasture treated at twice the commercial rate took nine weeks to recover whilst mature pasture took half that time. As the vigour of the desired species is also decreased by grazing and bruising (Miles and Isaacs 1969), an interval of at least three weeks should be left between grazing or cutting and spraying (Soper 1970).

The ability of the desired species to recover from spraying is generally considered to be greater in spring than in autumn, although Evans (1968) felt that autumn treatment would have a lower overall effect on grasses because they were not at their growth peak. Miles and Isaacs (1969) found that the effects of spring treatment lasted for three to four weeks compared to 12 weeks with autumn spraying. Soper (1970) has pointed out that as the decrease in herbage does not take place for about a week after treatment, the production loss can be minimized by grazing before the drop in yield occurs. However, this may lead to a longer recovery time for the pasture.

Regrowth of dock plants may occur after pastures and crops have been treated with Asulox. The regrowth may be

from seeds or unaffected dormant buds on the crowns of the larger, more complex roots. Either buried soil seed or seed transported into the area from outside may be responsible for dock reinfestation. Where density-dependent mortality is operating, pre-emergence spraying may allow the growth of seedlings which would otherwise have been suppressed (Harper 1957A), particularly if the adult population was suppressing seedling growth as well. However, Savoury and Soper (1970) found that reinfestation from seeds was negligible because although the number of seedlings (which were found on bare patches) fluctuated wildly, natural mortality was very high. Seedling reinfestation is only significant in run-down pastures. Here, seedling docks are able to establish themselves within 16 weeks of spraying (Miles and Isaacs 1969). This agrees with Harper's (1957B) statement that reinvasion by a weed will take place unless the environment is changed by management. Because docks can only become established from seed where open habitats exist (Cavers and Harper 1964) the bare patches left by dying docks should be resown if the pasture or crop is not aggressive enough to move into these areas rapidly (Lescar 1970). Lescar (1970) also suggests that good management, the use of fertilizer and good husbandry practices are necessary. However, Griffiths (1968) found application of nitrogen before spraying had no effect.

Re-establishment of dock plants from seed may be prevented to some extent by the residual effects of Asulox after spraying. Harper (1957B) points out that *R. obtusifolius* seeds are usually found buried in the soil between 8 and 10 centimeters deep and that chemical spraying would have little

effect on these seeds. The residual effect of Asulox seems to act principally on emerging seeds. Ball *et al.* (1965) found that seedlings failed to emerge in dilute solutions of Asulox. Ford and Combellack (1966) were using Asulox doses between two and a quarter and three times the commercial rate and found that seedlings emerging under field conditions showed a pink colouration and died quite quickly. How long the residual effects of Asulox last is not known although Ford and Combellack (1966) reported residual activity in seedlings up to 32 weeks after spraying.

Less than 10% of sprayed plants recover. Docks with smaller roots usually fail to survive treatment (Evans 1968). Well established plants with dormant "root buds" situated on large, complex, semi-independent roots may survive (Savoury and Soper 1970) and need retreatment. Blair (1968) observed such regrowth in the form of new leaves on surviving root stocks. Dormant buds probably survive because they are not active and have no leaves at the time of spraying or because they are shielded from the spray and translocation to them from other parts is low because of the partial independence of the roots. Such plants can be effectively treated the following year by re-spraying.

(f) The long-term benefits of using Asulox: In the long term, the use of Asulox results in yield increases and improvements in the sward composition. Savoury and Soper (1970) found that even moderate removal of docks increased grass yield after two months. Courtney (1970) also found that sites with the best control showed the greatest improvement in dry matter yield, although the increase in grass yield did not always compensate for the lost production

by docks. Sward composition is improved by spraying with Asulox; for example, the growth of *Holcus lanatus* is depressed (Miles and Isaacs 1969). Weeds other than docks are also suppressed. These include *Avena fatua* and many polygonaceous weeds, for example, *R. acetosella*.

(g) The use of Asulox to control docks in other crops: This discussion has been primarily oriented towards grazing and cropping farms. However, Asulox tolerant plants also include sugar cane, linseed, bushfruits and potatoes, the last two of which are relevant to New Zealand conditions. Asulox has also been used successfully to control docks in orchards.

(h) The toxicity of Asulox and its persistence in soil: The dangers of the herbicide are relatively small. Ball *et al.* (1965) report that it had low toxicity to fish and mammals.

Tests conducted by May and Baker showed it had low toxicity to birds, and at concentrations of 1 to 2 per cent was practically non-toxic to honey bees.

Ball *et al.* did not state the time for its breakdown in the soil although they mentioned that two closely related chemicals, M & B 9057 and M & B 8882 break down rapidly. It is probable that at least a year is required for the complete breakdown of Asulox, as Ford and Combellack (1966) reported that it exhibited residual activity on seedlings 32 weeks after being sprayed.

(i) The use of Asulox in New Zealand: In New Zealand approximately one-third of the area infested with docks to a level where chemical control is economic is being

treated with Asulox. Of this area about 66% is pasture, 20% lucerne and about 5% red clover. The remaining small percentage is made up of horticultural crops, nurseries, white clover etc.

(3) Future Directions for Herbicidal Research

Future weed control methods have two principal problems to deal with. The first of these is the problem of the direct competition of weed plants with desired species. The control of nearly all docks which are competing with or lowering the quality of any crop is already feasible with a combination of carefully timed cultural and herbicidal control techniques. The inherent stability of weed populations, which is principally maintained by seed dormancy (Harper 1957A), presents a much greater problem.

The direction that weed control programmes will probably take towards further solutions of the first problem will centre on the discovery and testing of new compounds. Secondary to this will be an attempt to understand the mechanisms of selective foliar absorption of these chemicals and their translocation and modes of action within the plant. The long and short term side effects, particularly to soil microflora, will have to be understood better than they are at present, as well as the time new compounds remain in the soil.

Once plants have become established and the soil seed reserves built up, a stable situation ensues which is extremely difficult to disturb. This stability will probably have to be disrupted with a combination of minimum

cultivation techniques, dormancy breaking chemicals or herbicidal applications at the time of seedling emergence. Harper (1957B) suggested that there was a need for dormancy breaking chemicals. Chancellor (1970) has recently reiterated this need, and stated that recent work indicated that treatments to stimulate dormant seed to germinate might be developed. Progress towards finding such chemicals has not been great. One of the few successful programmes is described by Eplee (1975), who found that ethylene gas will effectively stimulate the germination of witch weed *(Stiga asiatica)* seeds under field conditions. He believes that the techniques developed will completely control witch weed in the United States.

Harper (1957B) expressed his concern for the action of herbicides in upsetting the natural balance. Apart from some of the more obvious problems associated with the use of herbicides, the evolution of herbicide resistant weeds is important. Harper pointed out that weeds which suffer 100% mortality after herbicide application before seeding cannot evolve herbicide resistance. Therefore the continued use of chemicals which are only suppressive should be avoided.

The more immediate requirements of chemical weed control researchers is for broader approaches to problems of weed control which rely on a knowledge of weed biology to suggest new control measures, rather than to account for their action retrospectively.

IV. THE BIOLOGICAL CONTROL OF DOCKS

The biological control of these species may be

possible in the future if pathogens or grazers which are specific to them can be discovered.

Inman (1969) has reported that in preliminary experiments with the rust fungus *Uromyces rumicus* (Schum.) Wist. reductions of up to 10% have been achieved in the reproductive potential of *R. crispus* after infection. A more significant effect was in the reduction of plant vigour. Only 43% of plants which had been infected during spring and summer had resumed growth by the following spring, compared to 95% in the control. The defoliation resulting from infection had a seriously debilitating effect on root stock vigour. The selections for strains with higher pathogenicity was being carried out in 1969.

Swatonek (1972) has completed preliminary work testing the sorrel leaf beetle *(Gastroidea viridula* Dog.) as a biological control agent for *Rumex* spp. The beetle has three to four generations per year in the field, each female laying 100 to 600 eggs. In trials the adults consumed up to 23 cm^2 and the larvae 5 cm^2 of *R. obtusifolius* leaves in a generation. As the primary food of this beetle is *Rumex* spp., it has good potential as a biological control agent for these species.

I have been unable to find any references to the chemical and physical defense mechanisms of docks.

Docks are hardly ever seen in fields where sheep have been grazing. It is possible that the introduction of sheep into fields normally grazed by cattle would reduce the level of dock infestation. This would probably be most effective during the spring and summer, at the peak growth of the docks. Sheep graze on the younger leaves of dock plants,

closely enough to damage the apical meristems. The docks, which are unable to replace their food reserves, exhaust their resources and are severely reduced in size and may die. Sheep do no permanent damage to *R. acetosella*.

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APPENDIX 1. PLOT DETAILS.

Species	Plot	No of quadrats (quadrat	Total No of plants at initial survey	Mean No of plants per quadrat	Density per square meter	Standard deviat- of mean plants per quadrat
	3	10	100	10	1000	3.1
R. acetosella						
	4	18	100	5.6	560	3.4
R. crispus	1	62	84	1.4	1.4	1.2
	2	12	100	8.3	33.2	1.5
R. obtusifolius	5	9	87	9.6	9.6	1.4
	6	62	85	1.4	1.4	2.2

APPENDIX 2. SURVEY DATES FOR LIFE HISTORY AND SURVIVORSHIP DATA.

Plot 3. R. acetosella

1 March, 23 March,24 June, 11 December, 1974.

21 February, 12 July, 1 November, 1975.

Plot 4. R. acetosella

23 March, 10 June, 14 December, 1974.

9 March, 16 August, 1975.

Plot 1. R. crispus

6 May, 15 November, 1974.

10 March, 11 September, 1975.

29 February, 1976.

Plot 2. R. crispus

28 March, 7 June, 16 October, 1974.

20 February, 9 September, 10 April, 1975.

4 November, 1976.

Plot 5. R. obtusifolius

2 March, 24 May, 6 October, 1974.

13 February, 15 September, 1975.

10 March, 28 May, 4 November, 1976.

Plot 6. R. obtusifolius

6 May, 15 November, 1974.

3 July, 12 December, 1975.

APPENDIX 3. SPEARMAN'S RANK CORRELATION COEFFICIENT FOR THE RELATIONSHIP BETWEEN REPRODUCTIVE EFFORT AND PLANT ENERGY (estimated by root energy). (See Fig. 21).

Species	Field plot no.	Spearman's rank correlation coefficient.	Significance level	Sample size
R. crispus	1	1.00	0.05	4
	2	0.93	0.05	5
R. obtusifolius	6	0.91	0.05	6
	5	1.00	0.01	5

The negative relationship between "modified" reproductive energy and root energy is significant for all four field plots.

APPENDIX 4. TOTAL JOULES PER HARVEST FOR *R. acetosella* PLANTS UNDER THREE STRESS TREATMENTS.
Three plants have been sampled at each harves for each treatment.

Stress treatment	Harvest								Mean
	1	2	3	4	5	6	7	8	
High	6.3	7.0	22.7	28.6	38.3	42.5	48.6	47.7	35.4
Medium	7.9	52.4	51.5	80.2	118.3	140.1	374.8	183.6	160.3
Low	46.9	81.5	89.5	161.5	290.9	344.3	687.2	379.3	335.9
Days after first harvest	0	15	45	62	84	98	109	123	

Regression equations:

		$s_{b_{Y.X}}$
High stress	$\log Y = 0.86 + 0.008X$	0.0009
Medium "	$\log Y = 1.23 + 0.010X$	0.0020
Low "	$\log Y = 1.69 + 0.009X$	0.0011

Significancesof the differences between slopes:

H-M $t = 1.33$ NS
H-L $t = 0.67$ NS
M-L $t = 11.95$ $P<0.01$

APPENDIX 5. RAW DATA USED TO CALCULATE THE ALLOCATION OF ENERGY TO SEXUAL REPRODUCTION IN *R. acetosella* PLANTS UNDER THREE STRESS TREATMENTS. (See table 20).

		Stress Treatment								
		High			Medium				Low			
Harvest no.		5			5	6	6		8			
Plant no.		3			2	2	3		2			
females	VO	0.2		(1.0)	2.1	-	2.4	(3.0)	0.6			(0.2)
	SD	3.9		(18.6)	0.1	4.9	3.2	(5.4)	1.3			(0.8)
	RP	5.9		(28.0)	1.4	7.9	12.1	(14.1)	7.8			(5.4)
	RPLVS	3.2		(15.2)	1.6	2.7	13.1	(11.4)	7.4			(5.1)
	LVS	3.2		(15.2)	15.6	2.0	15.5	(21.5)	26.4			(18.1)
	RTS	4.5		(21.4)	32.1	7.9	27.6	(44.5)	102.3			(70.3)
Harvest no.		6			7	8			7	7		
Plant no.		1			2	2			2	3		
males	VO	-		-	0.5	5.0		(3.3)	28.0	4.2		(8.3)
	FLW	0.1		(0.8)	1.1	1.7		(1.6)	1.4	2.3		(1.0)
	RP	3.9		(32.0)	6.8	6.0		(7.6)	13.7	25.5		(10.3)
	RPLVS	-		-	32.4	-		(19.3)	-	7.6		(2.0)
	LVS	2.4		(19.7)	35.4	8.7		(26.3)	56.3	7.5		(16.8)
	RTS	5.8		(47.5)	27.2	43.0		(41.8)	150.1	84.5		(61.8)

Figures in brackets show mean percentages for seed or flower. Figures shown are joules. FLW=flowers, VO = vegetative offspring, SD = seed, RP = reproductive panicle, LVS = leaves, RTS = roots.

APPENDIX 6. TOTAL LEAF LENGTH OF R. acetosella VEGETATIVE OFFSPRING RELATED TO VEGETATIVE OFFSPRING ENERGY (See Fig. 24).

Total leaf length (mm)	Energy (joules)
85	0.71
112	1.16
154	1.78
187	2.31
324	4.45
750	7.12
644	7.65
813	10.59
985	11.75
1290	15.31
1441	18.69
1689	18.96
1700	22.07
1990	24.03

Regression equation:

Total leaf length = 26 plus 80.5 energy in joules

APPENDIX 7. PERCENTAGE ALLOCATION TO VEGETATIVE OFFSPRING IN R. acetosella PLANTS WITHOUT FLOWERS. (See table 19).

Stress treatment		Energy (joules) allocated to VO, LVS and RTS in seperate plants								Mean	Mean as a percentage of total allocation	Standard deviation of mean
High	VO	0.1	0.9	0.1	1.8	0.9	1.8	1.8	0.4	1.0	9.0	0.7
	LVS	3.4	3.1	5.5	3.9	3.0	2.5	4.2	4.8	3.8	33.9	0.9
	RTS	3.3	2.8	4.2	5.2	7.4	6.9	9.6	10.7	6.3	57.1	2.7
Medium	VO	0.1	0.5	2.8	1.7	1.6				1.3	3.0	0.8
	LVS	4.8	18.1	33.7	14.0	21.2				18.4	41.6	9.4
	RTS	4.9	8.8	40.3	24.3	43.7					55.1	20.4
Low	VO	0.3	1.3	2.6	24.3	23.1	3.8	23.0		11.2	8.3	11.0
	LVS	21.7	13.2	22.1	51.2	49.9	55.6	49.8		37.6	33.8	16.5
	RTS	2o.6	15.9	76.0	65.9	131.0	91.0	236.3		90.9	58.0	554.4

VO = vegetative offspring, LVS = leaves, RTS = roots.

APPENDIX 8. ALLOCATION OF ENERGY TO VEGETATIVE OFFSPRING IN R. acetosella PLANTS WITH FLOWERS

Stress treatment	Percentage allocated					Mean	SD
High	3.6	0.01				3.6	-
Medium	3.2	2.0	6.6	3.9		3.9	1.7
Low	1.5	7.5	3.8	5.2	0.2	3.6	2.5

F value between parents with flowers and without flowers = 1.6, NS.

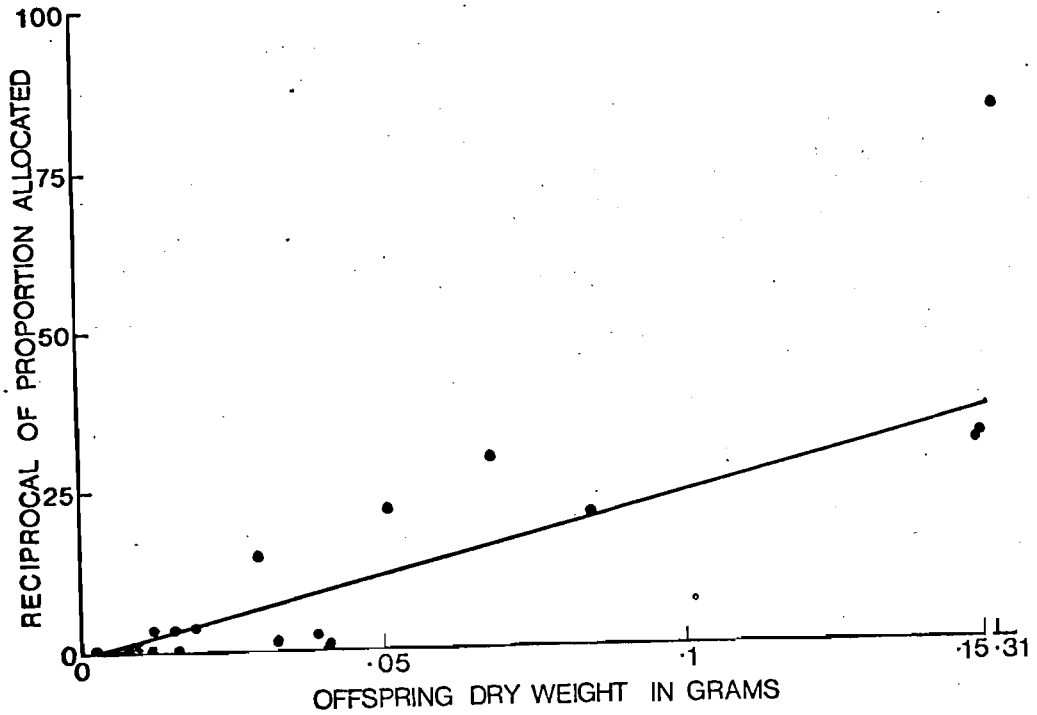

Fig. 32. Proportion of parental resources allocated to vegetative offspring in R. acetosella. Graph shows reciprocal plot of proportion allocated. See Appendix 9 for raw data

APPENDIX 9. PROPORTION OF PARENTAL RESOURCES ALLOCATED TO OFFSPRING. (See Fig. 25).

Sample number	Offspring dry weight (grams)	DPM (offspring) / DPM (total) / offspring weight *	Reciprocal of *
6	0.04109	1.560	0.64
10	0.01518	2.270	0.44
15	0.03302	0.969	1.03
25	0.01381	2.484	0.40
26	0.00209	3.166	0.32
27	0.06857	0.035	28.57
29	0.01239	0.308	3.25
30	0.05176	0.046	21.74
31	0.01686	2.438	0.41
32	0.08451	0.048	20.83
33	0.31954	0.012	83.33
37	0.00980	1.122	0.89
45	0.02973	0.067	14.93
53	0.01563	0.256	3.91
57	0.04152	0.963	1.04
60	0.01900	0.263	3.80
64	0.03282	0.884	1.13
68	0.03917	0.434	2.30
72	0.15453	0.032	31.25
92	0.15500	0.031	32.26

Regression equation: $\frac{1}{Y} = -2.2 + 257X$ $S_{b_{Y.X}}$ 18.73

See Fig. 32.

APPENDIX 10. ALLOCATION OF RESOURCES BY A SINGLE *R. acetosella* PARENT TO VEGETATIVE OFFSPRING OF VARIOUS SIZES. (See Fig. 26).

Offspring dry weight (grams)	DPM (offspring) / DPM (total) * offspring weight	Reciprocal of *
0.01686	0.4546	2.19
0.01239	0.4219	2.37
0.01680	0.2286	4.37
0.02090	0.0734	13.62
0.05176	0.0240	41.67
0.08451	0.0489	20.45
0.31954	0.0491	20.36

Regression equation: $S_{b_{Y.X}}$

$$\frac{1}{Y} = 12.01 + 40.11X \qquad 54.21$$

APPENDIX 11 . PROPORTION OF OFFSPRING RESOURCES ALLOCATED TO PARENTS. (See Fig. 25).

Sample Number	Offspring dry weight (grams)	DPM (parents) / DPM (total) ÷ parent weight
8	0.05208	0.0515
12	0.03305	0.1767
19	0.05149	0.1771
35	0.04119	0.0244
44	0.01427	0.0650
78	0.09224	0.0202

Regression equation: $s_{bY.X}$

$Y = 0.13 + 0.87X$ 1.32

APPENDIX 12. THE DISTANCE TRAVELLED BY RUMEX SEEDS IN A WIND TUNNEL (See Fig. 28).

Distance in cm	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	MEAN
R. acetosella	1	1	2	6	6	20	11	13	11	9	8	1	3	4	1	1	1	0	1	35.1
R. crispus without perianth segments	0	3	4	16	24	23	16	12	2											28.9
R. crispus	0	18	5	6	14	18	18	15	14	10	1	1	1							36.2
R. obtusifolius	0	1	7	14	25	25	16	5	5	2										23.6
R. obtusifolius without perianth segments	0	0	0	3	10	11	29	17	11	8	6	3	1	0	1					38.8

APPENDIX 13. PERIODS FOR WHICH SEED OF EACH SPECIES REMAINED AFLOAT (See Fig. 29).

Period in hours	0	.17	2	4	16	24	42	60	79	115	119	139
R. acetosella	13.6	5.0	4.4	4.2	3.6	3.4	3.2	2.8	2.6	2.0	2.0	1.8
	(4.4)	(2.5)	(2.7)	(2.0)	(2.2)	(2.2)	(2.0)	(1.2)	(1.3)	(1.5)	(1.5)	(1.2)
R. crispus	20.0	20.0	20.0	20.0	20.0	20.0	19.6	18.6	17.0	9.2	7.6	6.0
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.4)	(0.5)	(1.9)	(1.8)	(1.0)	(1.4)
R. obtusifolius	20.0	20.0	20.0	20.0	20.0	20.0	19.4	17.0	7.0	2.8	2.4	2.0
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.5)	(0.8)	(4.4)	(3.2)	(2.4)	(1.2)

Means of five groups of 20 seeds are shown.
Brackets show standard deviation of means.

APPENDIX 14.GERMINATION OF SUBMERGED SEEDS

Species	R. acetosella	R. crispus	R. obtusifolius
No seeds germinating in each flask after fourteen days.	22 45 18 10 35	0 20 10 5 0	70 80 85 90 75
Mean	26	7	80
SD	13	6	7

APPENDIX 15. PERCENTAGE GERMINATION OF SEED ON PANICLES CUT AT DIFFERENT STAGES OF SEED MATURITY. (See Table 24).

Developmental Stage	R. crispus	R. obtusifolius
Flowering	0 0 0 0 0 (0.0)	0 0 0 0 0 (0.0)
Green seed	0 0 0 0 0 (0.0)	34 8 0 0 48 (18.0)
Mature, brown seed	90 74 92 60 70 (77.2)	50 88 92 82 74 (77.2)

Figures show percentage germination for 50 seeds.

Brackets show means for each developmental stage.